PHILOSOPHICAL TRANSACTIONS

OF THE

ROYAL SOCIETY OF LONDON

SERIES B VOLUME 235

BIOLOGICAL SCIENCES

1950–1951

Published for the Royal Society by the
Cambridge University Press
London Bentley House, N W 1
New York 32 East 57th Street, 22

1951

PRINTED IN GREAT BRITAIN AT
THE UNIVERSITY PRESS, CAMBRIDGE

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The Committee appointed by the *Royal Society* to direct the publication of the *Philosophical Transactions* take this opportunity to acquaint the public that it fully appears, as well from the Council-books and Journals of the Society as from repeated declarations which have been made in several former *Transactions*, that the printing of them was always, from time to time, the single act of the respective Secretaries, till the Forty-seventh Volume, the Society, as a body, never interesting themselves any further in their publication than by occasionally recommending the revival of them to some of their Secretaries, when, from the particular circumstances of their affairs, the *Transactions* had happened for any length of time to be intermitted And this seems principally to have been done with a view to satisfy the public that their usual meetings were then continued, for the improvement of knowledge and benefit of mankind the great ends of their first institution by the Royal Charters, and which they have ever since steadily pursued

But the Society being of late years greatly enlarged, and their communications more numerous, it was thought advisable that a Committee of their members should be appointed to reconsider the papers read before them, and select out of them such as they should judge most proper for publication in the future *Transactions*, which was accordingly done upon 26th of March, 1752 And the grounds of their choice are, and will continue to be, the importance and singularity of the subjects, or the advantageous manner of treating them without pretending to answer for the certainty of the facts, or propriety of the reasonings contained in the several papers so published, which must still rest on the credit or judgment of their respective authors

It is likewise necessary on this occasion to remark, that it is an established rule of the Society, to which they will always adhere, never to give their opinion, as a Body, upon any subject, either of Nature or Art, that comes before them And therefore the thanks, which are frequently proposed from the Chair, to be given to the authors of such papers as are read at their accustomed meetings, or to the persons through whose hands they received them, are to be considered in no other light than as a matter of civility, in return for the respect shown to the Society by those communications The like also is to be said with regard to the several projects, inventions, and curiosities of various kinds, which are often exhibited to the Society, the authors whereof, or those who exhibit them, frequently take the liberty to report, and even to certify in the public newspapers, that they have met with the highest applause and approbation And therefore it is hoped that no regard will hereafter be paid to such reports and public notices, which in some instances have been too lightly credited, to the dishonour of the Society

THE SKULL OF THE FOETAL NARWHAL, *MONODON MONOCEROS* L

By NELLIE B EALES, D Sc Lond, *Zoology Department, University of Reading*

(*Communicated by F J Cole, F R S —Received* 12 *December* 1949)

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Understanding of the evolution of the mammalian orders and families, and of the relationships between members of an order, is often illuminated by a study of the development of the skull in the foetus This account is the first description of the foetal narwhal The material is extremely rare and the author is indebted to Professor L R Wager for the collection of the specimens when he was in Greenland as a member of the Courtauld Expedition in 1935–6 The chondrocranium and osteocranium of two early narwhal foetuses were investigated by dissection and by the preparation of models constructed from transverse sections of the head

The narwhal is a highly specialized Cetacean In the adult it differs from all other mammals in the complete absence of hairs, and from other Odontoceti in that instead of numerous similar teeth on both jaws, it has one very long straight tusk in the upper jaw in the male, and a pair of short tusks or none in the female, neither sex having teeth in the lower jaw Sections of the younger foetus, however, exhibit hairs on each side of the mandible, indicating that the narwhal is a typical mammal in this respect Continuous dental laminae in upper and lower jaws, with papillae for six pairs of teeth in the maxillae, and for two pairs in the mandibles, show that the specialized dentition of the adult is a modification of the more generalized foetal dentition

The study leads to the conclusion that the narwhal is more closely related to the Delphinidae than to the Phocaenidae, and that it approaches the Delphinidae through *Globiocephala*

Introduction

The material used for the present study consisted of two foetal narwhals, brought from Greenland by Professor L R Wager, who was the leader of the Courtauld Expedition to Kangerdlugssuak Fjord from 1935 to 1936 Knowing that I was interested in the foetal stages of rare mammals, Professor Wager undertook, before sailing, to look out for these specimens and bring back any he thought suitable for investigation He was able to collect three seal and three narwhal foetuses The Eskimo are accustomed to remove foetuses from

Vol. 235 B 621 (Price 7s 6d) 1 [Published 17 October 1950

female narwhals and take them home to their children, who wrap them up and carry them in their arms as dolls

The narwhals were obtained just inside the mouth of the main fjord The animals are of vital importance to the Eskimo, since the ivory of the tusk is an essential part of the harpoon, oil is extracted from the blubber for fuel, and the flesh is used for food for men and dogs Wager writes, 'It is no easy matter to hunt successfully a large narwhal weighing about a ton, and two or three men have to collaborate Towards the end of the second summer they had so much meat that they hunted only the male narwhal, and having killed it, took only the ivory tusk In a year they killed 410 seals, 28 bears and 40 narwhals'

No special method of preservation was employed, the foetuses were immersed in alcohol, the intense cold retarding putrefaction and giving excellent fixation of the tissues

The data concerning the three specimens, henceforward called A, B and C, are as follows

A Mother shot at base, 29 May 1936 Female foetus 137 mm long, 30 mm broad at the widest part of the abdomen, 32 mm high Well preserved, but the colourless skin was torn in places This specimen was sectioned and the skull was modelled

B Mother caught by Eskimos at Kangerdlugssuak, 28 June 1936 She had a young narwhal about 120 cm long with her, but this was not caught The uterus of the mother contained a foetus 150 mm long, 24 mm broad, 40 mm high, and the specimen on arrival was much distorted by compression The head of this specimen, which was also a female, was dissected

C Mother shot at base, 28 July 1936 Male foetus 280 mm long, 60 mm broad, 70 mm high This specimen has not yet been investigated, as it was considered too old for the present study

HISTORICAL

Foetal narwhal material is very rare, and little has been written upon the few specimens known The range of the species is very limited, few animals reaching farther south than 65° N latitude The males are hunted for their ivory as well as for their flesh and blubber, but the female with its small and usually concealed tusk is of little value, and the Eskimo hunters leave it alone, unless they are short of meat Narwhal tusks have been known since the twelfth century

The first record of a narwhal foetus was made by Frederic Ruysch, the founder of a famous anatomical museum in Amsterdam In his *Thesaurus Anatomicus* (1714) he figured a foetal narwhal suspended in a bottle It had hairs on the top of its head, nostrils and large round eyes! The umbilical cord was present

About 1736 Anderson saw a narwhal taken in the Elbe at Hamburg He described it as a female, with two tusks, 7 ft 5 in and 7 ft long, and it contained a foetus, about which, however, he gave no details

A century later Rapp (1837) referred to the teeth of a foetal narwhal, noting the two pairs of teeth in the upper jaw

Sir William Turner wrote several papers on narwhals, describing in 1872 a male foetus of 181 mm length, with two pairs of teeth in the upper jaw, and in 1878 another foetus 1625 mm long, the teeth being again described Between these two dates Gervais (1873) gave an account of a foetus 1150 mm long and of its teeth It was almost at term, the only reference to age in any of the above foetuses, though according to Turner's measurements it was 500 mm too short for a full-term foetus However, since the duration of the gestation period is unknown, it is not possible to estimate the age of foetuses by Mackintosh & Wheeler's graphical method (1929) In 1879 Wilson described the retia mirabilia of the narwhal from a partly decomposed specimen 1606 mm in length

Fraser (1938), in his paper on the vestigial teeth of the narwhal, examined a male foetus 520 mm in length, and found two pairs of symmetrical teeth in the upper jaw, the first or tusk-forming pair being longer and better developed than the second pair Neither showed signs of spiral structure Comparison with an older foetus 1588 mm long, and with post-natal stages, indicated that asymmetry in size and length occurred later in both sexes in the tusk-forming pair, but not usually in the second or vestigial pair, which abort from the posterior end of the alveolus, leaving a shallow depression in the maxilla The vestigial tooth may fall out on one side or the other, but the left is not affected, as far as Fraser could determine, by the great development of the tusk on that side

The American Museum of Natural History possesses two narwhal foetuses, one a full-term foetus, from which the skeleton has been prepared, measuring 1500 mm in length The second, said to be between 3 and 4 months old, was embalmed and is 225 mm long

Finally, Huber (1934) made a partial dissection of the head of a full-term narwhal foetus, working chiefly on the superficial muscles and the blow-hole mechanism

Thus the knowledge derived from these twelve foetuses amounts to little more than an account of the teeth and of the blow-hole mechanism

METHODS

Foetus A, the better preserved and smaller specimen, was sectioned The head, measuring 32 mm. in length, was cut off, decalcified, embedded in celloidin, and sectioned at $40\,\mu$ by Dr Keith Richardson, of University College, London The sections were then stained as follows

Ehrlich's acid haematoxylin, 2 % in distilled water, for 12 hr Rinsed in distilled water, differentiated in weak acid alcohol, blued in tap water, rinsed again in distilled water

Counterstained in orange G erythrosin* for 30 min

Dehydrated in 30, 50, 90 % alcohol, and transferred to a mixture of absolute alcohol 3 parts, chloroform 1 part

Cleared in the following mixture, made up to soften, but not to dissolve, the celloidin

creosote	40 ml
bergamot oil	30 ml
xylene	20 ml
origanum oil	10 ml

Each section was coaxed on to the surface of a slide, drained of oil, rinsed quickly in xylene from a drop bottle, and mounted in Canada balsam under a weighted cover-slip

---

* Tischutkin's formula orange G, 4% aq , 10 ml , erythrosin 10% aq , 2 ml

I am grateful to Dr Richardson for cutting the sections and for suggesting the method of staining, which proved successful

The skeletal parts of the head were drawn under the Edinger projection apparatus, using a Zeiss planar lens, giving a magnification of 12 5 Beeswax plates 1 mm thick were employed for the models Separate models of the chondrocranium and combined chondrocranium and osteocranium were made, also an enlarged model, magnified twenty-five times, of the membranous labyrinth and auditory ossicles

Foetus B was dissected The head was distorted by pressure and parts of the body had been damaged, but it was possible to make a fair dissection of the skull

Foetus A

The eye is closed The single blow-hole is almost transversely placed on the anterior aspect of the head, so that it is directed straight forwards The mouth is ventral and not quite terminal The flippers are sufficiently transparent to show the fingers through the skin The posterior apertures are sunk in a median elongated depression and consist of an anterior swollen vulva and immediately posterior to it the anus On either side of the outer wall of the vulvar area is a mammary slit Thus the female external genitalia are well developed

Figure 1 Foetus A in right ventro-lateral view Note the severed umbilical cord, posterior to which are the vulva and the anus The skin is torn in places (Magn × 1)

The tail has the horizontal fluke formed, but there is only a trace of division into two halves The vertebral portion is laterally compressed with a mesial skin fold on dorsal and ventral sides Ventrally this skin fold extends forwards almost to the anus, dorsally it fades out just over half-way up the back, its total length being 71 mm There is no dorsal fin

The age of the foetus is unknown According to Turner (1878) a full-term specimen would be about twelve times the length of this foetus This is the youngest foetus recorded

Skull model

Although this was the youngest specimen, calcification was well advanced and the general characters of the genus were developed The basi-cranial axis is almost flat, the basi-facial axis sloping upwards to the nasals and making an angle of about 135° with the former

Owing to the high position of the external nares the basi-facial line is thus raised above the basi-cranial axis instead of being below it as in most other mammals The upper jaw, however, is dropped, and whereas the brain case curves upwards anteriorly, the palate curves downwards. The anterior part of the nasal tube is thus almost vertical, and the nasal septum long and upright The occipital plane makes an angle of 70° with the basis cranii The roof of the skull is smoothly rounded, with a large anterior fontanelle, and there are lateral vacuities where ossification is imperfect

Chondrocranium (figures 2, 3 and 4)

The basis cranii (*p*) is thick and solid, and is flanked by two large occipital condyles (*oc*), which, although more ventrally placed than in most mammals, do not quite meet The pars lateralis (*pl*) of the occipital cartilage meets its fellow to form a tectum posterius (*tp*) over the foramen magnum, though the paired supraoccipital portions of the arch are discernible A small fenestra is present anterior to the fusion There is an extensive ossification of the supraoccipital cartilages, forming a median supraoccipital bone (*sob*), with paired posterior prolongations on either side of the fenestra In section the bone is wedged into the cartilage and appears capstan-shaped The paracondylar process (*pcp*) is large and inflated, it exhibits an ossification centre (exoccipital) which is broadened out on the outer face of the skull, but is of small size intracranially The styloid process of the hyoid apparatus is attached to the paracondylar process In a recess postero-ventral to the intracranial ossification lies the hypoglossal foramen (*hf*), single on each side as in *Phocaena* The large jugular foramen (*fj*) is the jagged gap between the auditory capsule and the occipital

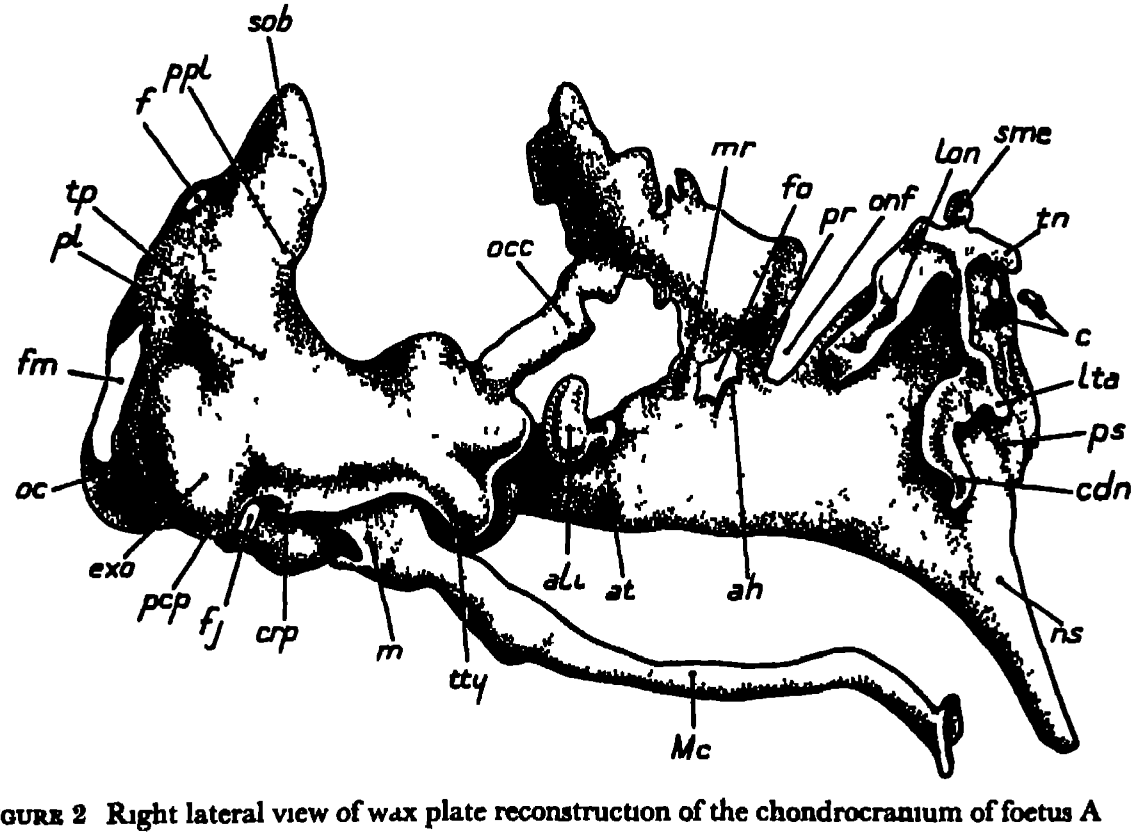

FIGURE 2 Right lateral view of wax plate reconstruction of the chondrocranium of foetus A (Magn ×4 5)

cartilage The parietal plates are joined to the auditory capsules by the prefacial and postfacial (parieto-capsular) commissures, and there is a vestige on the left side of an orbitoparietal commissure (*copv*) The wall of the skull laterally is substantial, and the tegmen tympani reinforces the prefacial attachment by forming a lateral prefacial commissure. The orbital cartilages are linked with the auditory capsules by orbito-capsular commissures (*occ*) The basal plate narrows between the auditory capsules and is strongly ossified ventrally as the basi-occipital bone (*bo*) This bone is, as it were, wrapped round the cartilage, so that it appears laterally in cranial view, while its posterior portion sends out a pair of bony extensions which partly overlap the auditory capsule on its ventral face The notochord is intrabasal, but takes a sinuous course through the cartilage Each basicochlear fissure (*bcf*) is well defined, in its middle part the sides are parallel, but it broadens posteriorly, where the basi-occipital ossification shows on the brain-case floor, forming an ovate hole, lateral to which lies the basivestibular commissure (*bvc*)

The lamina supracochlearis (*lsu*), or dorso-lateral projection of the basal plate, is short, and extends like a shelf over the anterior portion of the auditory capsule, but without attachment to it, the capsule being sunk below it There is thus no alicochlear commissure, and the lamina supracochlearis merely links the trabecular and parachordal portions of the chondrocranium The processus alaris (*pal*) has united with the ala temporalis (*at*) to form a club-shaped structure, ossified at its free end as the alisphenoid bone (*ali*) The ala temporalis is imperforate, and there is therefore no alisphenoid canal for the orbital artery The alisphenoid is a cartilage bone and there is no trace of membrane bone in this region The root of the processus alaris is pierced by the carotid foramen (*fc*), which is well within the basal plate Anterior to the processus alaris is the large gap transmitting the first branch of the trigeminal nerve (later this will form the foramen lacerum anterius or sphenoidal fissure), posterior to it is the foramen lacerum medium for the second branch of the same nerve De Beer (1937, p 401) states that the lamina supracochlearis is part of the basal plate and the alicochlear commissure the hinder region of the trabeculae Both lie dorsal to the auditory capsule In the narwhal foetus the lamina supracochlearis is well developed, but the alicochlear commissure is absent As noted by de Burlet in *Lagenorhynchus* (1914*b*) the parietal plate and lamina supracochlearis are slightly larger on the left side than on the right

The pituitary fossa is shallow The foramen hypophyseos is no longer perforate, but traces of it are visible in the sections There is no dorsum sellae and the crista transversa is weakly defined

The preoptic and metoptic roots of the orbital cartilage are relatively slender, and do not show any unusual features The optic foramen (*fo*) is large, and mesially the trabecular plate is hollowed out for the optic chiasma There is a very small nodule of cartilage beneath the optic nerve, projecting downwards from the anterior border of the foramen, probably representing an ala hypochiasmatica (*ah*) The remnants of the orbito-parietal commissure are weak, and consist of slender pieces of cartilage lying flat against the cranial face of the frontal and parietal bones They do not make a connexion with the parietal plate The orbito-capsular commissure (*occ*) is, however, complete The slight ossification on the edge of the optic foramen postero-mesially is the anlage of the orbitosphenoid bone (*ors*)

The orbito-nasal fissure (*onf*) is large and ovate, but there is no sphenethmoid commissure

The most remarkable portion of the chondrocranium is the nasal region, which is compressed laterally and truncated anteriorly, giving the skull a flat, depressed front, partly concealed in the flesh by a cushion of connective tissue, loaded with fat, which rounds it off Its support is the massive cartilage of the septum nasi (*ns*) approximately triangular in shape, with its long axis almost vertical, but sloping slightly forwards at its ventral end The height is twice the antero-posterior length, and it overhangs the lower jaw There is no cranial rostrum since the septum does not project anterior to the blow-hole The dorsal or cranial end of the septum is narrow, the foramen olfactorium advehens (*fol*) forming a longitudinal slit on each side of it. (There are no olfactory lobes in the brain, or olfactory nerves, and

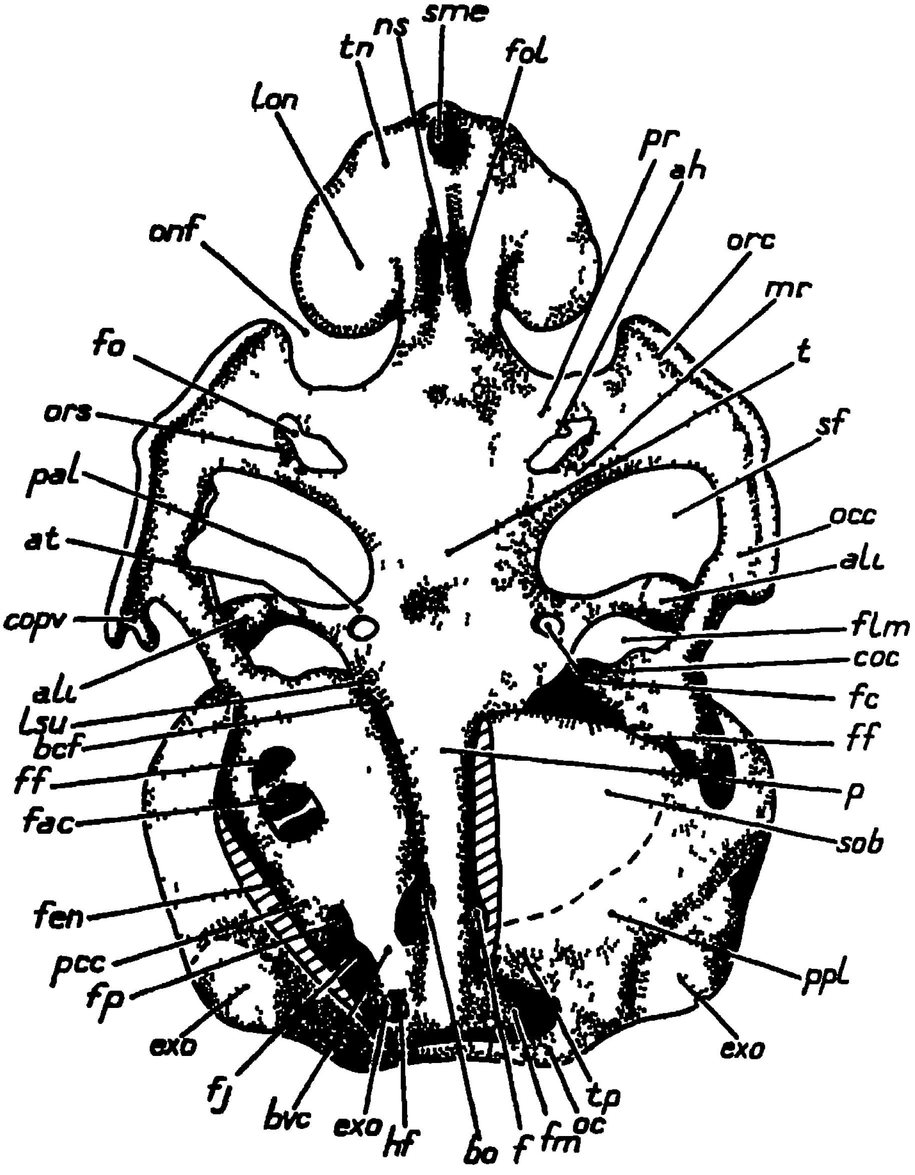

FIGURE 3 Dorsal view of model of chondrocranium of foetus A The *tectum posterius* has been cut on the left side to expose the auditory capsule and basal plate (Magn × 4 5)

a cribriform plate is absent) The lamina orbito-nasalis (*lon*) lies parallel with the septum nasi, and has the form of a flat plate projecting laterally, and turned ventralwards and mesialwards on its edge as a vestigial lamina transversalis posterior, which does not, however, reach the septum nasi The latter and the pair of orbito-nasal cartilages unite anteriorly and rise up in a crest surmounted by a median spina mesethmoidalis (*sme*) The tectum nasi (*tn*) forms a shallow roof over the nasal cavities, directing the blow-hole forwards and slightly upwards No epiphanial foramen is present The paries nasi (*pns*), figure 8, flanking each nasal cavity, is extremely slender, and bends mesialwards as the lamina transversalis anterior (*lta*), which completes the ring by touching, but not fusing with, the nasal septum Pendent from it posteriorly, and lying flat against the septum, is a cartilage bent at a right angle, consisting of the anterior paraseptal cartilage (*ps*), and the remnant of the cartilago ductus nasopalatini (*cdn*) There is no trace, however, of Jacobson's organ

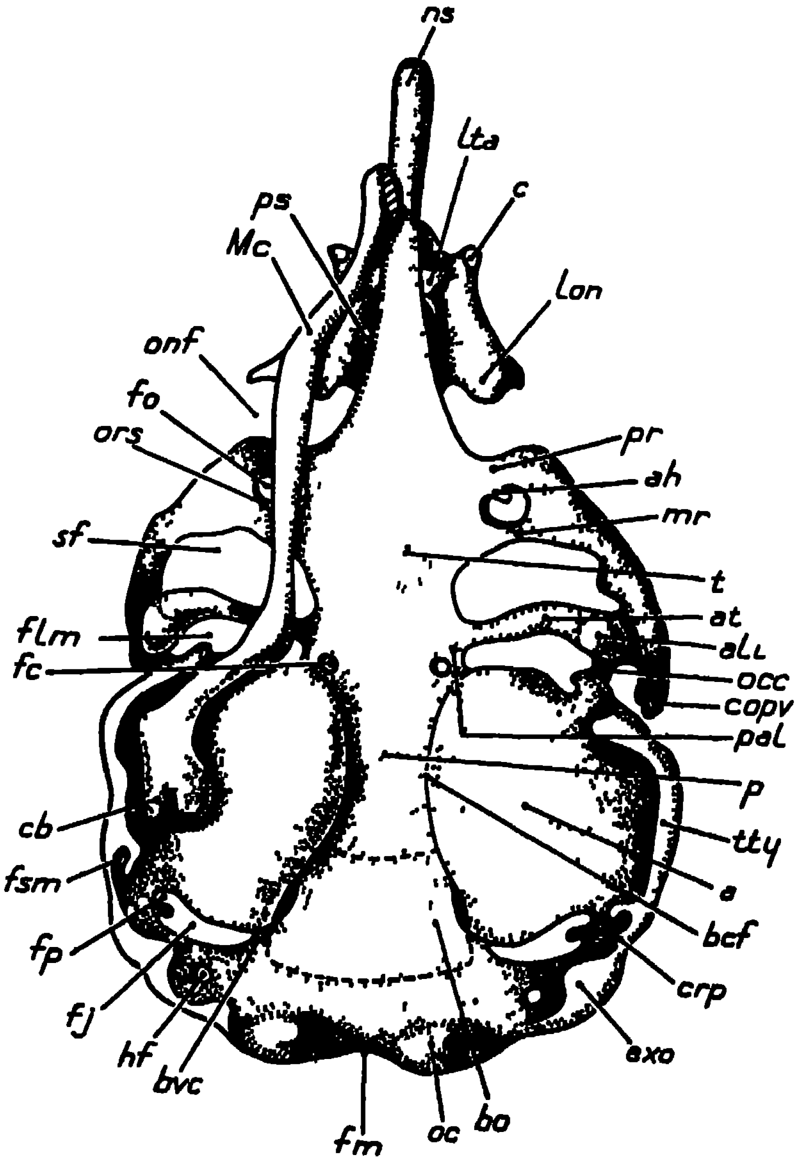

FIGURE 4 Ventral view of model of chondrocranium of foetus A Meckel's cartilage has been removed on the left side of the specimen. (Magn × 4 5.)

The nasal tube has thus no postero-ventral skeletal boundary, and posterior paraseptal cartilages are absent Two isolated nodules of cartilage—*paranasals* (*c*)—are present on the side of each nasal tube, projecting forwards from the paries nasi There are lateral ingrowths in the mucous lining of the nasal tubes, representing the maxillo-turbinal folds, but these contain no cartilaginous supports

Meckel's cartilages (*Mc*) are slender twisted rods Each lies along the mesial face of the dentary bone, the ventro-lateral border of which is cup-shaped to receive it The anterior portion is curved downwards where the dentary narrows Here it is enclosed by the bone and becomes partially ossified (?medio-Meckelian), then breaks through the anterior end of the dentary, projecting beyond it and forming the major part of the symphysis The two cartilages diverge slightly anterior to the symphysis, and each ends freely Posteriorly Meckel's cartilage is linked with the auditory region (see below)

As is well known, the auditory capsule in the Cetacea is readily separable from the rest of the skull in the adult, owing to the fact that the fused petrosal and tympanic are attached to the other bones by membrane only In the foetus, however, before ossification in any part of the capsule has occurred, the cartilaginous capsule is linked with other parts of the chondrocranium at the following points

(1) Antero-laterally by the orbito-capsular commissure (*occ*) joining the orbital cartilage with the lateral wall of the auditory capsule

(2) Laterally and on the dorsal or cranial side by the prefacial (supra-facial) commissure, linking the side wall of the skull with the auditory capsule, anterior to the entrance of the facial nerve into the aqueductus Falloppii, and continuous laterally with the orbito-capsular commissure This is shown, but not lettered, in figure 3

(3) Laterally and ventrally by the lateral prefacial commissure, joining the tegmen tympani with the auditory capsule, the cavity in the cartilage between 2 and 3 known as the cavum supracochleare being occupied by the facial ganglion and the palatine branch of the facial nerve (see figure 4)

(4) Postero-laterally by the parieto-capsular (postfacial) commissure (*pcc*), forming the antero-lateral boundary of the foramen lacerum posterius, and joining the parietal plate and the capsule posterior to the internal auditory meatus

(5) Posteriorly by the basivestibular commissure (*bvc*), forming the mesial boundary of the foramen lacerum posterius, and running longitudinally instead of transversely as in most mammals

As already stated, the lamina supracochlearis overlaps, but does not fuse with the capsule wall, and there is therefore no alicochlear commissure, *sensu stricto* The basal plate is also free from the capsule, the mesial prefacial commissure being absent Thus the capsule is moored laterally and posteriorly, but not mesially, and has no attachment either to the trabecular plate (alicochlear commissure), or to the basal plate (mesial prefacial commissure)

The second peculiarity of the auditory capsule is its orientation It has swung round to a more transverse position in the Cetacea, so that the cochlear sac is antero-ventral and has sunk to a position slightly ventral to the basal plate, being partly covered by the projecting edge of the latter (lamina supra-cochlearis), while the canalicular portion is elevated to a postero-dorsal position lateral to the cochlear part

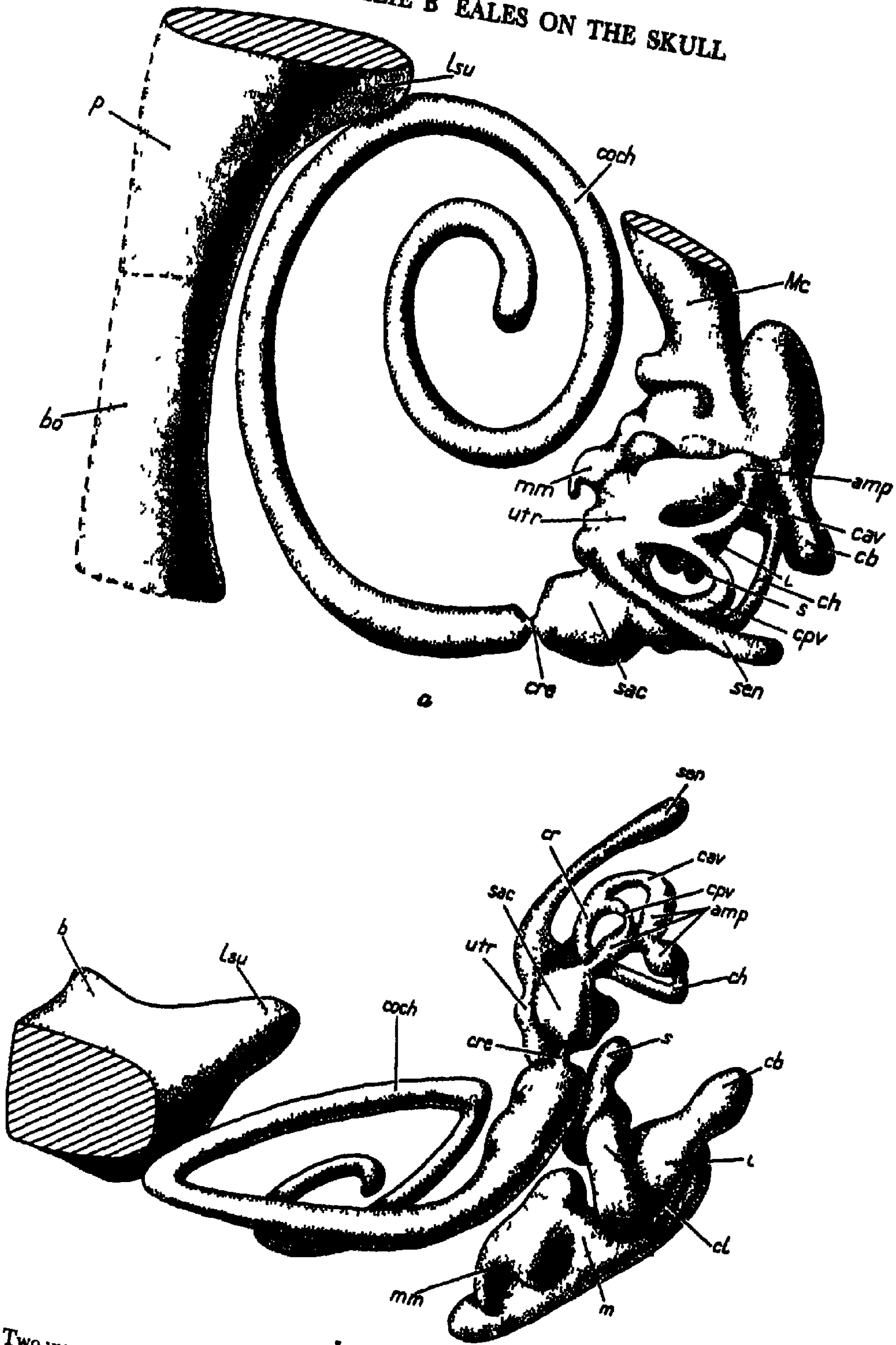

FIGURE 5 Two views of wax plate reconstructions of the membranous labyrinth and auditory ossicles of foetus A (Magn ×16) *a*, Dorsal view to show the relative size of the canalicular and cochlear portions of the labyrinth *b*, Posterior view to show the ossicles A portion of the basal plate has also been modelled to illustrate the sunken position of the auditory capsule and its contents

The foramen acusticum internum (internal auditory meatus) (*fac*) is a large irregular aperture situated between the cochlear and canalicular portions, it transmits the eighth nerve to the labyrinth, and is subdivided by a bar separating the cochlear and vestibular branches of the nerve The foramen for the facial nerve (aqueductus Falloppii) (*ff*) is anterior to the foramen acusticum internum and is separated from it by cartilage The foramen perilymphaticum (*fp*) lies on the anterior wall of the foramen lacerum posterius, (jugular foramen) appearing to be excavated from the latter The small foramen endolymphaticum (*fen*) is antero-lateral to it

The tegmen tympani (*tty*) is well developed at this stage, and extends downwards from the parietal plate, forming, as has been noted, the lateral prefacial commissure with the auditory capsule Its free posteroventral portion curves round the exit of the facial nerve, then runs back as a short projecting shelf towards the attachment of the styloid process of the hyoid This projection is the crista parotica (*crp*)

Auditory ossicles (figure 5)

These are at present pure cartilage Meckel's cartilage ascends towards the auditory region and through the connexion between its posterior portion (the malleus (*m*)) and the incus (*i*), makes contact with the skull, but there is no condyle as yet on the dentary bone Meckel's cartilage broadens posteriorly to form the globular head of the malleus for the socket on the body of the incus There is little evidence as yet of a saddle-shaped articulation, though the cup-shaped socket on the incus is sinuous At its posterior extremity there is continuity for a short distance with the incus, a condition that occurs in the early stages of development in other mammals Antero-dorsally a short processus brevis (lateral process) is forming, but there is no narrowing in the future neck region towards the formation of a processus gracilis The postero-ventral part bends sharply to form the arcuate manubrium (*mm*), which, even in the foetus, touches the small obliquely placed tympanic membrane by its tip

The incus is a sturdy cartilage, with an anterior hollowed surface for articulation and partial fusion with the malleus Its dorsal arm (crus breve) (*cb*) ascends dorso-laterally to fit into a depression, the fossa incudis, under the overhanging tegmen tympani of the skull, but there is no fusion of the cartilages The crus longum (*cl*) passes backwards and mesialwards towards the head of the stapes and there is here a nodule of cartilage that may represent an os orbiculare (processus lenticulare), though it appears to belong to the stapes rather than to the incus, and is partly continuous with the former

The stapes (*s*) is short and broad Its base fits neatly into the fenestra ovalis (vestibuli) Externally it looks solid, but in the sections it exhibits a small hole between the crura, not traversed, however, even in the foetus, by a stapedial artery

Rotation of the auditory capsule has brought the fenestra ovalis to a ventral position

The membrane bone representing the pre-articular (goniale of Gaupp) is described on p 17

Cartilage bones represented at this stage are the supra-occipital, ex-occipitals, alisphenoids, orbitosphenoids and basi-occipital The presphenoid and basisphenoid regions are not yet ossified

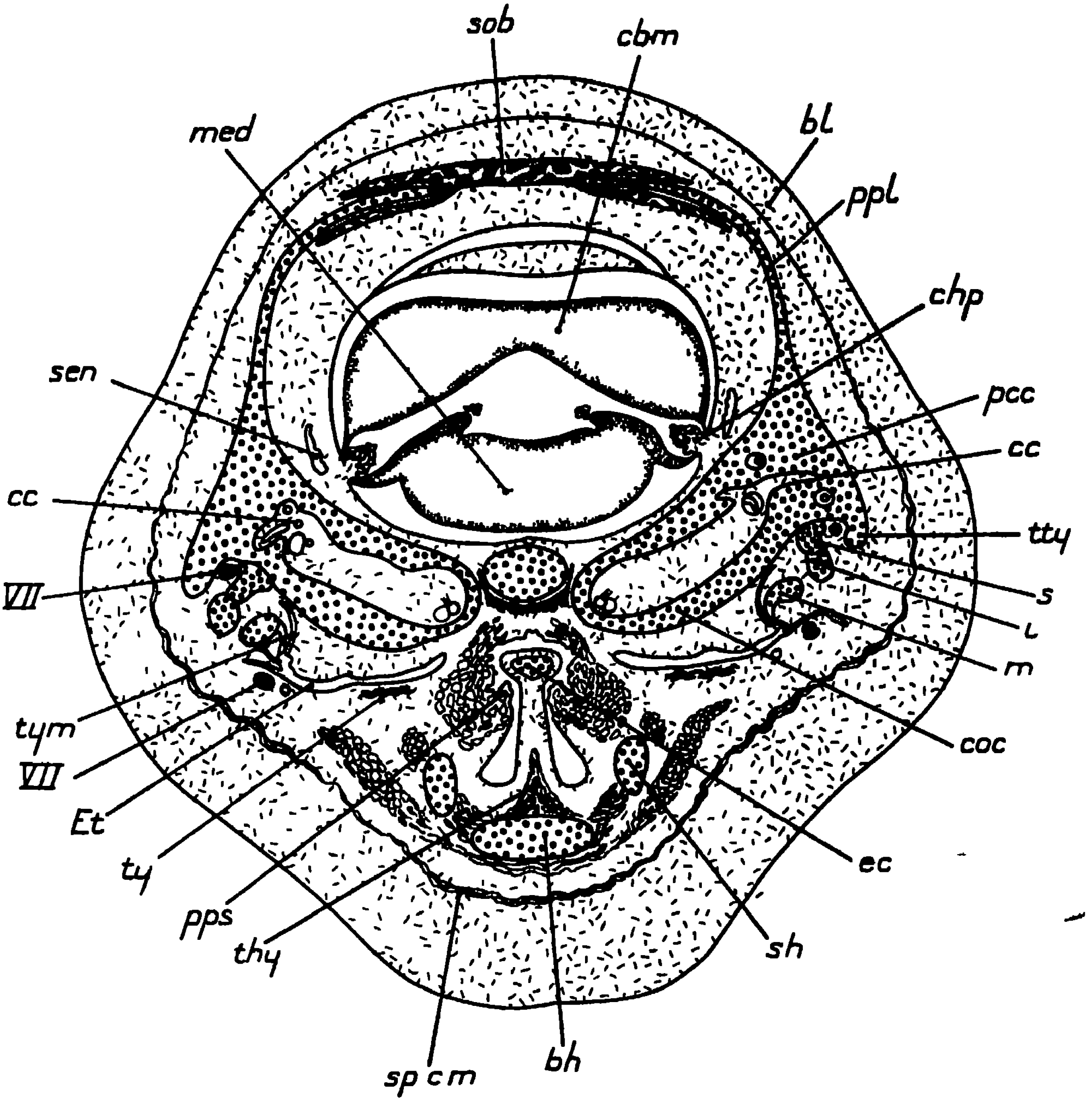

FIGURE 6 Foetus A Section 550, through the canalicular and cochlear portions of the auditory capsule, the ear ossicles and the intra-narial epiglottis Cartilage dotted, bone black dendritic, nerve solid black, muscle faintly lined, connective tissue and blubber with short, straight lines (Magn × 5 4)

Membranous labyrinth (figure 5)

An enlarged model, magnified 25 times, was made of the membranous labyrinth and auditory cartilages of the right side The labyrinth resembles that figured by Honigmann (1917) in *Megaptera* The cochlea (*coch*) is very large, being twice the width and three times the length of the whole of the canalicular portion Its two coils are widely spaced, and this is exaggerated in the model, since the scala tympani and scala vestibuli are not well defined, so that the ductus cochlearis alone was modelled The canalicular portion is small but normal The ampulla is as yet little wider than the canal it serves, but can be recognized by the presence of a crista ampullaris internally The utricle has an elongated macula acustica, and contracts into a ductus utriculo-saccularis, into it opens the slender duct of the bulbous saccus endolymphaticus (*sen*), which curves dorsalwards to lie alongside the brain, under the connective tissue that will later form the dura mater The saccule (*sac*) is small and has a macula acustica on its inner wall, it narrows and bends ventralwards as the canalis reuniens (*cre*), then expands into the ductus cochlearis, which performs two complete turns before ending blindly

Osteocranium (figures 7, 8 and 9)

All the main membrane bones are present at this stage, though some are very thin

The nasals (*nas*) are small bones, elliptical in contour, set on the summit of the head dorsal to the tectum nasi The pair do not make contact mesially and between and behind them the spina mesethmoidalis projects upwards

The premaxillae (*pmx*) are long, narrow shafts of bone, converging ventrally towards the nasal septum, but diverging dorsally where the maxilla forks round each premaxilla and runs alongside the nasal septum The premaxilla hardly reaches the edge of the upper jaw at this stage but it does appear on the palatal surface for a small area anteriorly, though recessed Since in the adult the premaxilla forms the lateral boundary of the nasal tube,

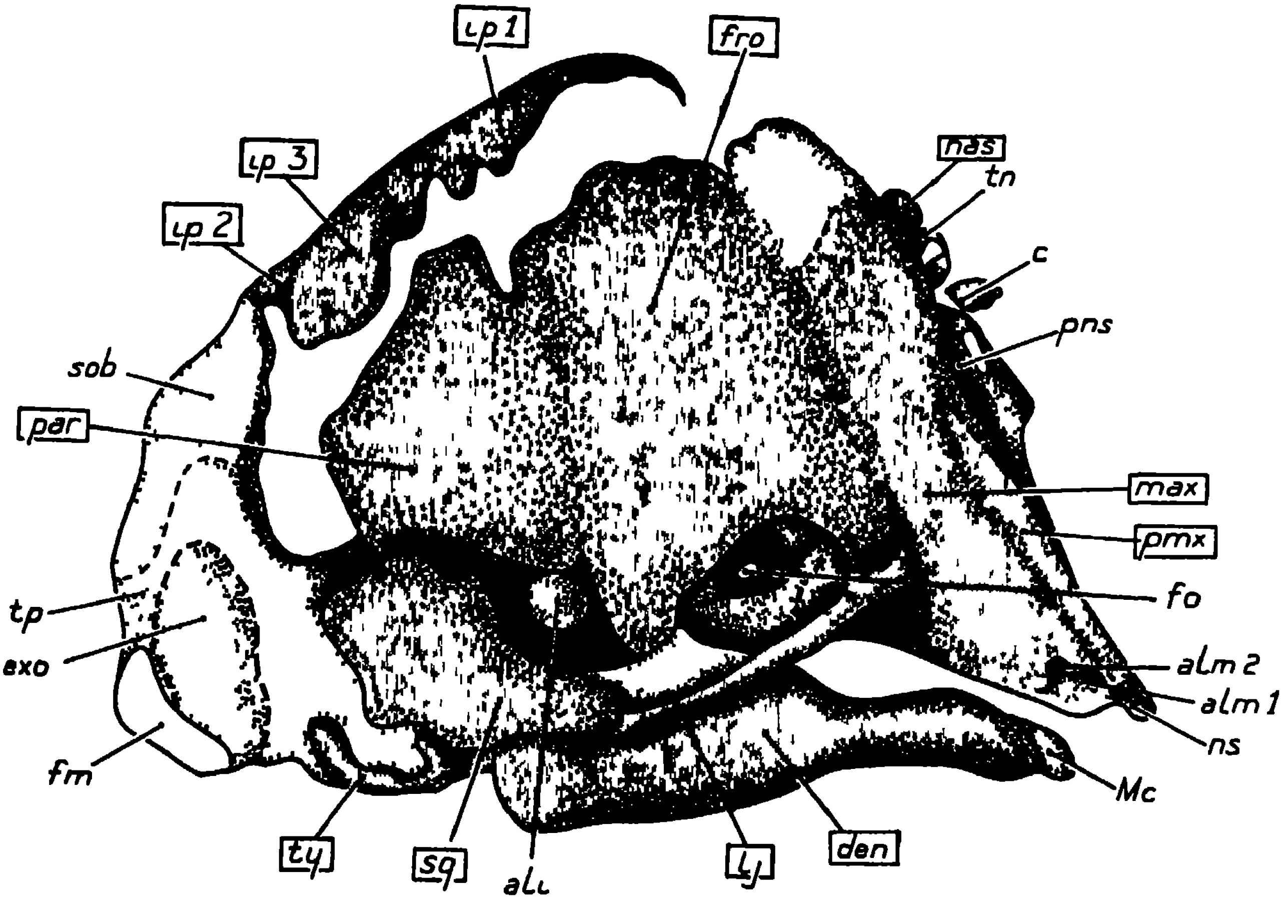

FIGURE 7 Foetus A Right lateral view of wax plate reconstruction of the chondrocranium and osteocranium The lettering for membrane bones has been enclosed in rectangles and the bones themselves finely stippled in this and some subsequent figures (Magn × 4 5)

some rearrangement of the bony tissue must occur in this region, and it would appear to be brought about by the premaxilla growing upwards and covering part of the maxilla See specimen B

The maxillae (*max*) are massive bones commencing close to the paries nasi and extending ventralwards towards the nasal septum, making contact with the latter about midway along its length Dorso-laterally each forms a very small part of the floor of the brain case, but it is more extensive on the face, where it overlaps the frontal, forks round the premaxilla as mentioned above, and reaches to the edge of the upper jaw, its palatal process forming the major part of the hard palate It has no zygomatic process but meets the lachrymo-jugal alongside the pre-orbital process of the frontal Antero-ventrally it is excavated to form two tooth sockets containing tooth papillae Maxillae, premaxillae and nasal septum are prolonged downwards, overhanging the receding lower jaw

The frontals (*fro*) are overlapped by the maxillae antero-ventrally but are free dorsally, they are therefore more extensive on the cranial than the facial aspect On the face each

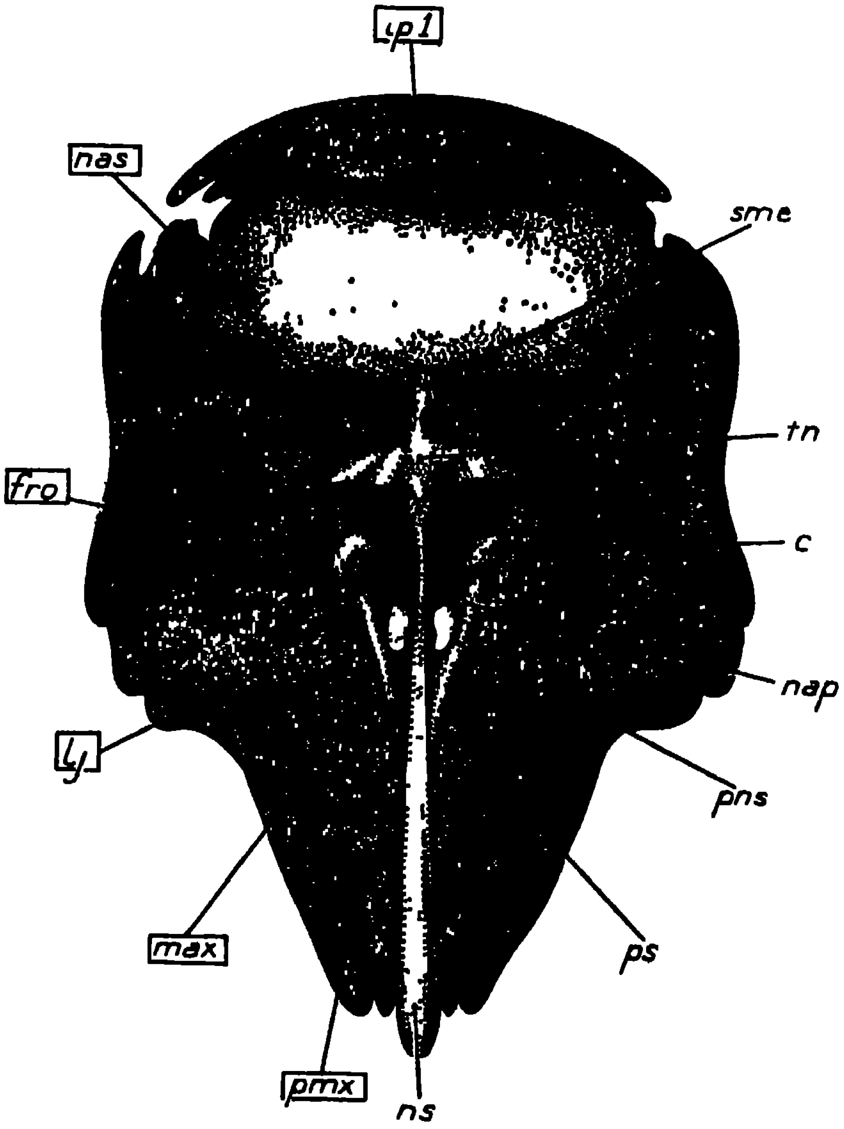

FIGURE 8. Foetus A Anterior view of the same model as figure 7 (Magn × 4 5)

frontal is heavily built ventrally where it is hollowed out for the eye, and becomes thinner in the upstanding shaft, forming a jagged side boundary to the superior fontanelle Pre- and post-orbital processes are well developed, the former meeting the maxilla and lachrymo-jugal, the latter hanging freely, the orbit being open posteriorly The low position and downward direction of the eye are very marked, even at this early stage On the cranial side the thin anterior shaft of the frontal reaches to the lamina orbito-nasalis, thus cutting off most of the maxilla from the brain case The orbital cartilage and part of the orbito-parietal commissure lie flat against the cranial face of the frontal posteriorly

The parietals (*par*) are small lateral bones making contact with the frontals on their anterior borders but otherwise surrounded by membrane The two parietals are widely separated by the large inter-parietal, so that, as in other Odontoceti, they never reach the vertex of the skull Ventro-laterally the parietal touches the bony alisphenoid On the cranial side the thin bar of the orbito- capsular commissure is attached to it, running longitudinally across it, and there is a remnant of an orbito-parietal commissure on the left side

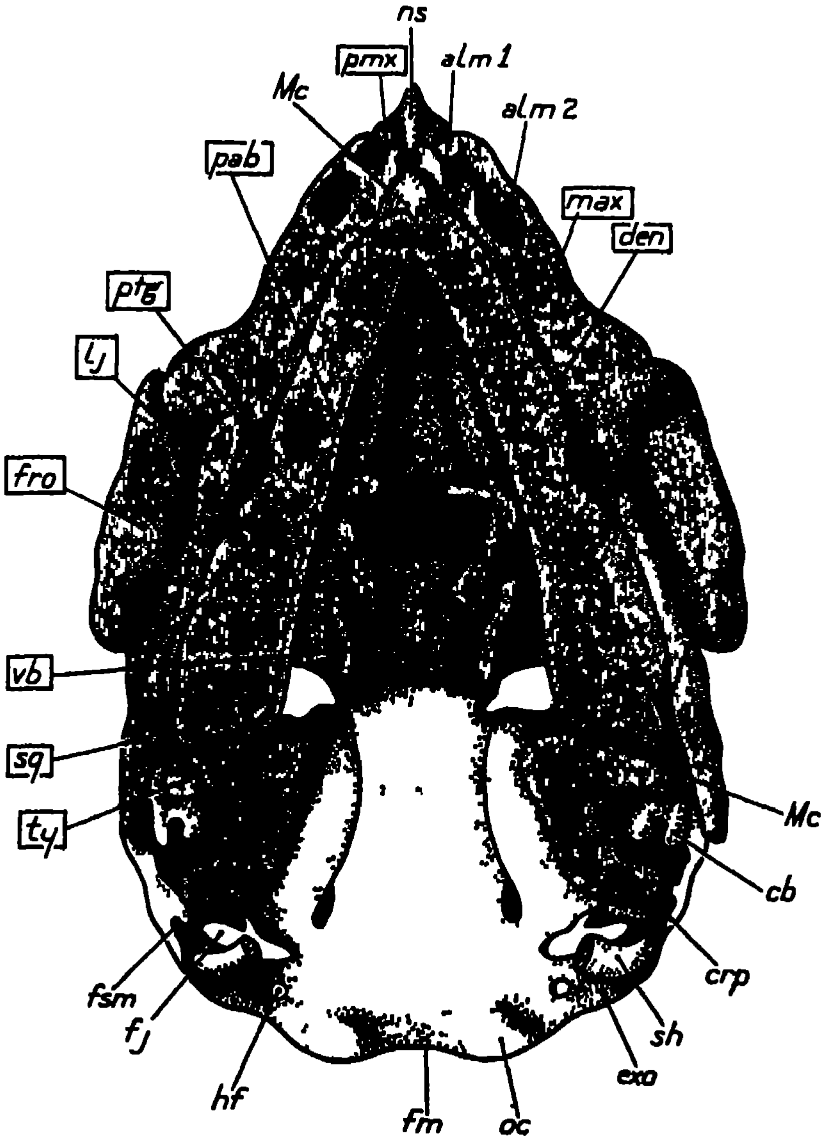

FIGURE 9 Foetus A Ventral view of the same model as figure 7 (Magn ×4 5)

The interparietal (*ip*) is the largest element in the osteocranium Posteriorly it ossifies from three centres, a pair of thin bony plates making contact with the supra-occipital, with a central plate partly overlapped by this pair Anteriorly there is a median, wide, curved flap, roofing in the skull behind the anterior fontanelle See specimen B and discussion on p 27

The lachrymo-jugals (*lj*) are slender bars of bone typical of the Cetacea, but differing from those of the porpoises and dolphins by being curved, as if they had been forced downwards and inwards by the overhanging eyeball There is no trace of fusion between jugal

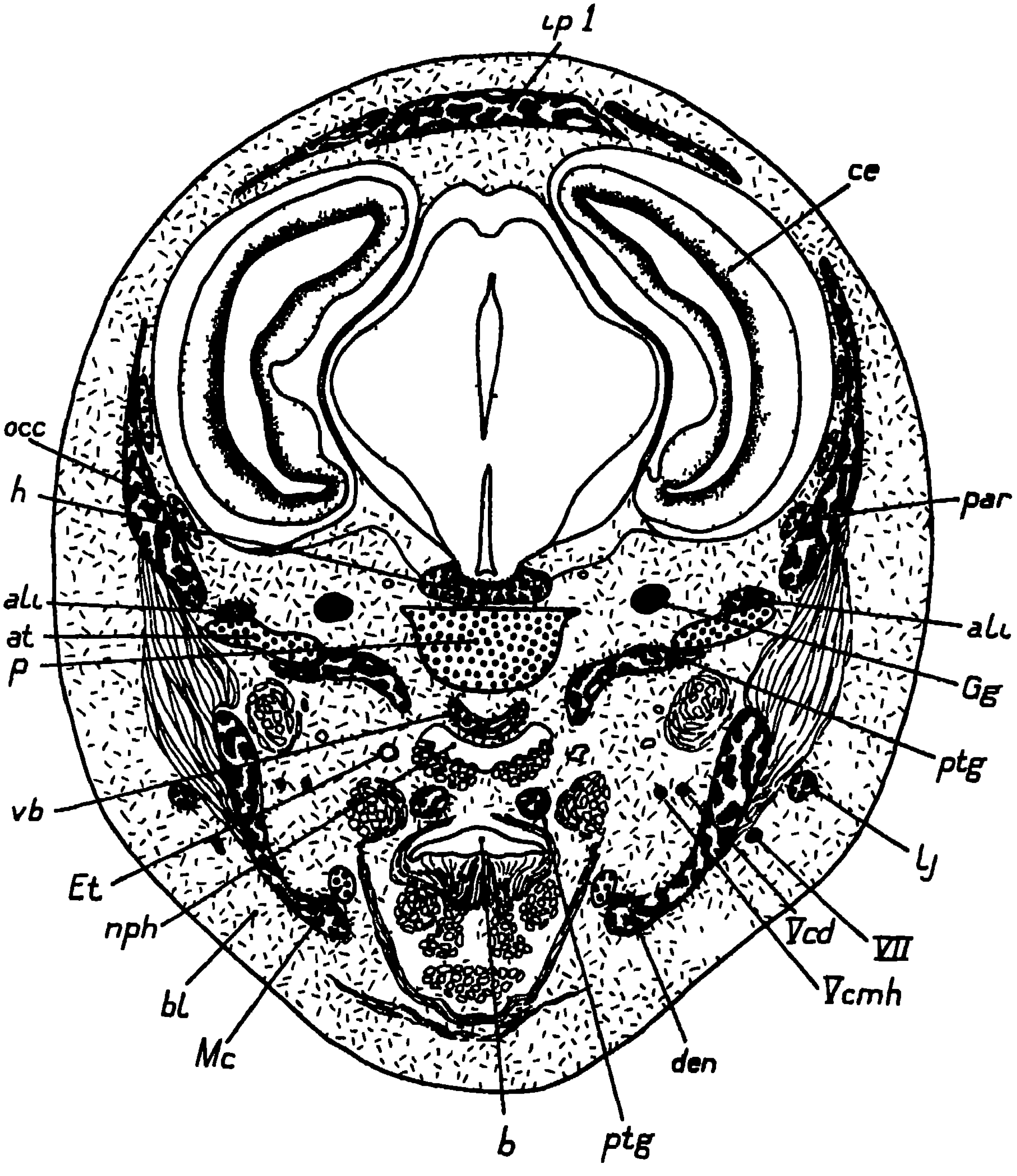

FIGURE 10 Foetus A Section 388, through the pituitary region (Magn ×5 4) Conventions as in figure 6

and lachrymal, and the lachrymal portion is imperforate Posteriorly there is a weak articulation with the forward shaft of the squamosal

The squamosals (*sq*) are articulated with the lachrymo-jugals, but otherwise are linked only with the chondrocranium They are small flat bones lying over the tegmen tympani Although the dentaries are well ossified their condyles do not as yet make contact with the squamosals, the glenoid surfaces of which have not yet shaped themselves

The tympanics (*ty*) are crescentic bones attached antero-laterally to the ventral side of the auditory capsules

There is no periotic ossification at this stage

Gomale In close apposition to the antero-lateral horn of each tympanic crescent, and between it and the cartilaginous malleus (proximal end of Meckel's cartilage), is a small membrane bone, the pre-articular or goniale of Gaupp In Cetacea this bone fuses with the tympanic, and from its close contact here there is every indication that it will do so

The palatines (*pab*) form only a very small portion of the sides of the hard palate as in the adult Their palatal processes extend mesialwards but do not meet mid-ventrally, and the vomer is exposed between them They are deeper than broad, the anterior portions running forwards as tapering shafts dorsal to the maxillae

The pterygoids (*ptg*) are larger than the palatines and act as supporters of the soft palate by means of their backwardly directed hamular processes The lateral portion develops ventrally to the ala temporalis, the anterior portion touches the palatine

The vomer (*vb*) is a large median bone closely pressed against the ventral side of the trabecular plate, dorsal to the palatal processes of the maxillae and hidden anteriorly by them

The dentaries (*den*) are massive bones of typical Cetacean shape, i e flat and high, with weak condyles and coronoid processes Anteriorly they become slender and curve ventralwards, stopping short opposite the alveolar region of the upper jaw, which overhangs them The condyles have not reached the squamosals Meckel's cartilages unite to form the anterior tip of the symphysis, but the dentaries join ventrally and form the posterior portion The hollowing out of the mesial face of the dentary for Meckel's cartilage has been described above The inferior dental nerve enters its foramen about halfway along the mesial surface of the bone On the dorso-lateral surface of the dentary there is a shallow alveolar groove (*ald*), which becomes more pronounced in Stage B See figures 12*c* and 14

All the membrane bones present in the adult, except the periotic, are in process of development in this foetus

Teeth

That two pairs of teeth are developed in the upper jaw of the narwhal has been known since C Mulder discovered them in 1835, and several later writers refer to or describe them Fraser (1938) described these teeth in the narwhal, and an account of his paper is given on p 3 Both the future tusk-forming pair (the left tooth of this pair actually becoming the tusk) and the second vestigial pair are present in the foetus The dental papillae for the first pair are equal, each lying in its dental sac in a hollow of the maxillary bone, and situated on the overhanging portion of the upper jaw (i e anterior to the symphysis rami) The second pair are also symmetrical in size and shape Posterior to them the tooth band extends for a considerable distance, and can be traced through 65 sections Thus the tusk forming pair occupy sections 111 to 132, the second pair 144 to 160, and the dental band continues to section 225 There are small dental papillae in the regions of sections 182, 191, 198 and 210, after which the band fades out These are so regular that each probably represents the *anlage* of a tooth, making a possible six pairs on the upper jaw

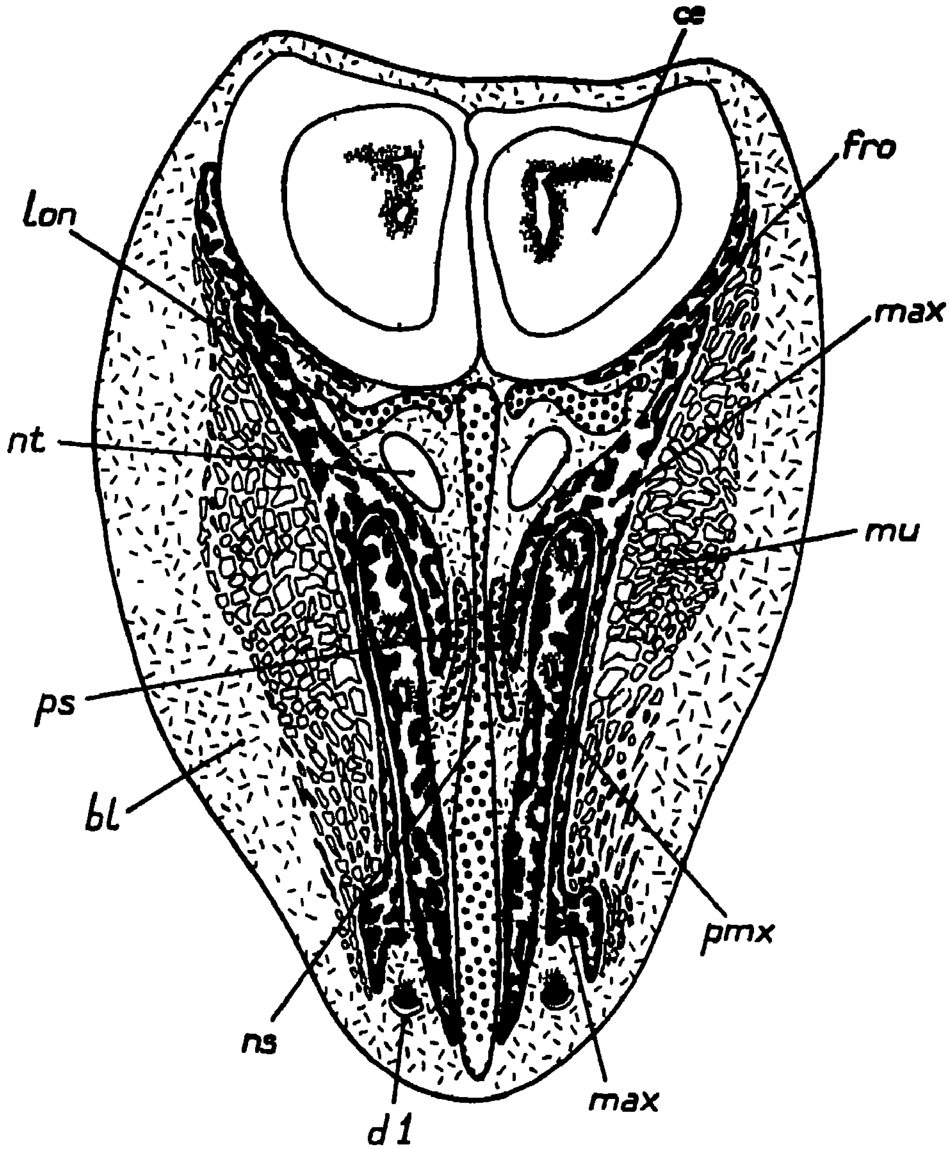

Figure 11 Foetus A Section 120 through the lamina orbito-nasalis, nasal septum and the tusk-forming tooth (Magn × 5 4)

On the lower jaw there is an invagination of the buccal epithelium running through 75 sections (162 to 237), with a dental papilla between sections 213 and 220, and another between 226 and 232 The model shows the corresponding alveolar groove on the dorso-lateral border of the dentary bone

In the foetus, therefore, there are signs of six pairs of teeth in the upper jaw and of two pairs in the lower jaw, and the maxilla and dentary are excavated for their reception

While investigating the dental lamina, hair germs were found in a regular series on each

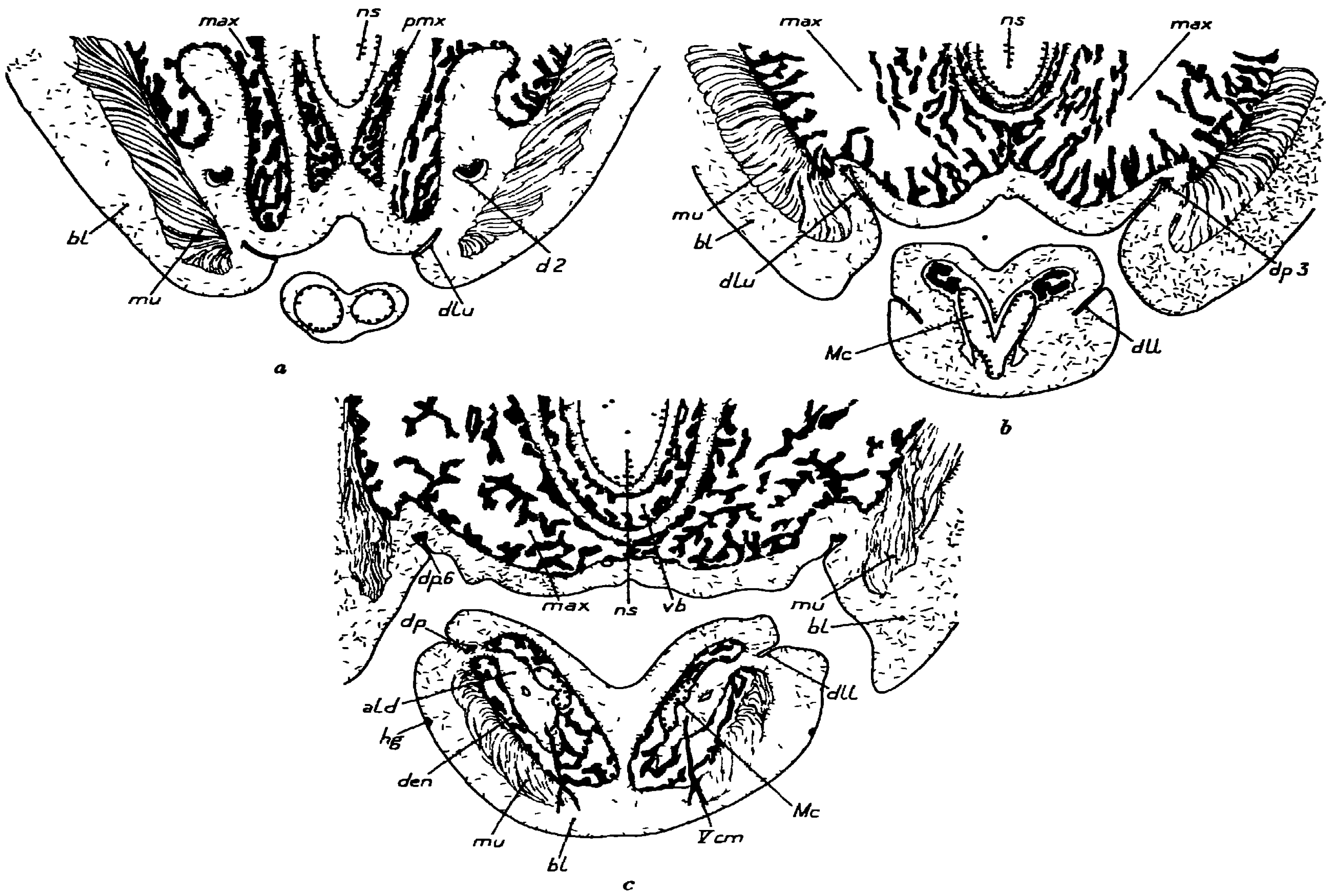

FIGURE 12 Foetus A Three parts of sections to show teeth and dental laminae For the tusk-forming tooth, see figure 11 *a*, Section 150 Second tooth and dental lamina in the upper jaw (Magn × 8 5) *b*, Section 182 Dental lamina, with third dental papilla in the upper jaw, and lamina in the lower jaw (Magn × 8 5) *c*, Section 215 Sixth dental papilla in the upper jaw In the lower jaw note the alveolar grooves in the dentary bones, the dental laminae and a dental papilla on the left side of the section Two hair germs are also present (Magn × 8 5)

side of the lower jaw There were seven pairs, one behind the other Beddard (1900) and Howell (1930*a*) state that the narwhal never has hairs at any stage of the life history They may not be fully developed, but remnants of them remain

Foetus B (figures 13 and 14)

The second foetus, also a female, measured only 13 mm longer than specimen A, and was probably therefore not much older Its skull, however, shows well marked advances in development In general, these changes are as follows

The skull has elongated in the antero-posterior direction, chiefly owing to the growth of the nasal septum, premaxilla and maxilla The cranium has become dome-shaped, and with the growth of the anterior region the nasal aperture is being pushed back on the head from a pre-orbital to a supra-orbital position In the adult it will become post-orbital

The cartilage bones have not extended their growth very much, but the membrane bones have spread, particularly the frontals, parietals and interparietals The anterior fontanelle now occupies the summit of the head, the lateral fontanelles have narrowed The interparietal, which in foetus A showed a tripartite ossification posteriorly, has now split into median anterior, paired postero-lateral and median posterior portions

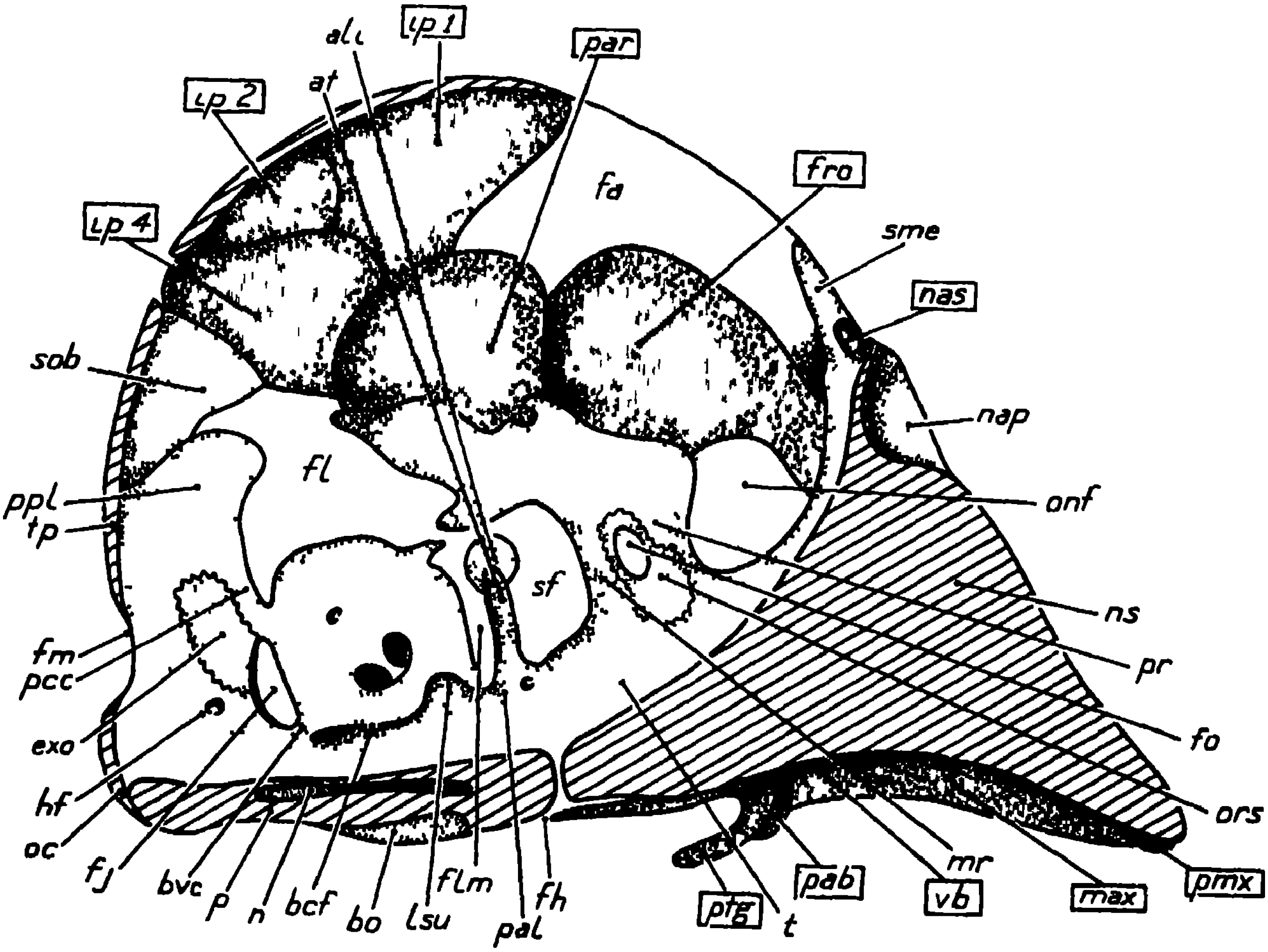

Figure 13 Foetus B Sagittal section of the skull, showing the interior of the brain case, after removal of the soft parts Cut surfaces are indicated by parallel lines Membrane bones have their letters enclosed in rectangles (Magn ×4)

After dissection the skull was bisected longitudinally and the brain removed to expose the remnants of the chondrocranium Interpretation was facilitated by light staining with safranin (1 % in 50 % alcohol)

Chondrocranium

The basis cranii is thick and shows the curved remains of the intrabasal notochord (*n*) The occipital condyles have fused ventrally The foramen hypophyseos (*fh*) is almost vertically placed and leads to a shallow sella turcica dorsally, while ventrally it is just covered by the bony vomer The trabecular plate increases in thickness as it extends forwards to form the septum nasi, a large triangular mass of cartilage rising up to the external narial aperture Laterally, in cranial view, the basivestibular commissure is still intact, but the orbito-capsular commissure has broken down at the middle, so that the process of isolation of the auditory capsule has begun In this stage it is moored by the basivestibular, parieto-capsular, prefacial and lateral prefacial commissures, though all of these are weaker The basicochlear fissure has narrowed, but the lamina supracochlearis is thicker Ossification has proceeded in the preoptic root of the orbital plate—orbitosphenoid bone (*ors*)—and the alisphenoid has spread

In the nasal region the lamina orbitonasalis has become thinner but has extended dorsalwards, so that the nasal bones are lower than the weak but tall spina mesethmoidalis The septum nasi has increased greatly in size by forward and downward growth, carrying with it the premaxillary and maxillary bones

Meckel's cartilage is still present on the inner face of the dentary, but it no longer projects at the symphysis

The chief developments at this stage are

The beginning of the isolation of the auditory capsules owing to the breakdown of the antero-lateral mooring cartilages

Increased ossification of the orbital cartilage to form the orbito-sphenoid bone

Great increase in size of the nasal septum

Osteocranium

The nasals (*nas*) have grown very little, but the maxillae have made contact with them The premaxillae (*pmx*) have become furrowed longitudinally, they have extended anteriorly with the growth of the nasal septum, but not yet posteriorly, so that the shafts running laterally to the nasal aperture and reaching to the nasals in the adult have not formed Their palatal extent resembles that of older stages The maxillary fork mesial to the premaxilla, seen in foetus A, has weakened The maxillae (*max*) overlap the frontals, on the palatal aspect they exhibit a pair of alveolar grooves which reach along their whole length

The frontals (*fro*) are partly covered by the maxillae, and overlap the parietals They do not meet mid-dorsally and there is still a large anterior fontanelle Their pre- and postorbital processes have become more massive, pushing the eyeball downwards and outwards and forming a semi-tubular projection on the side of the head

The parietals (*par*) are somewhat sunken, being covered on their edges by the frontals, squamosals and interparietals They are entirely lateral in position Dorsally they reach to the anterior fontanelle, posteriorly they form the anterior border of the lateral fontanelle

The interparietal (*ip*) is the largest bone in the skull, and overlaps the parietals, but meets the frontals and supra-occipital, though development on the two sides of the head is not uniform It shows division into four parts, anterior and posterior median bones and a pair of lateral ones The lateral bones make contact with one another mid-dorsally See foetus A, and Discussion, p 27

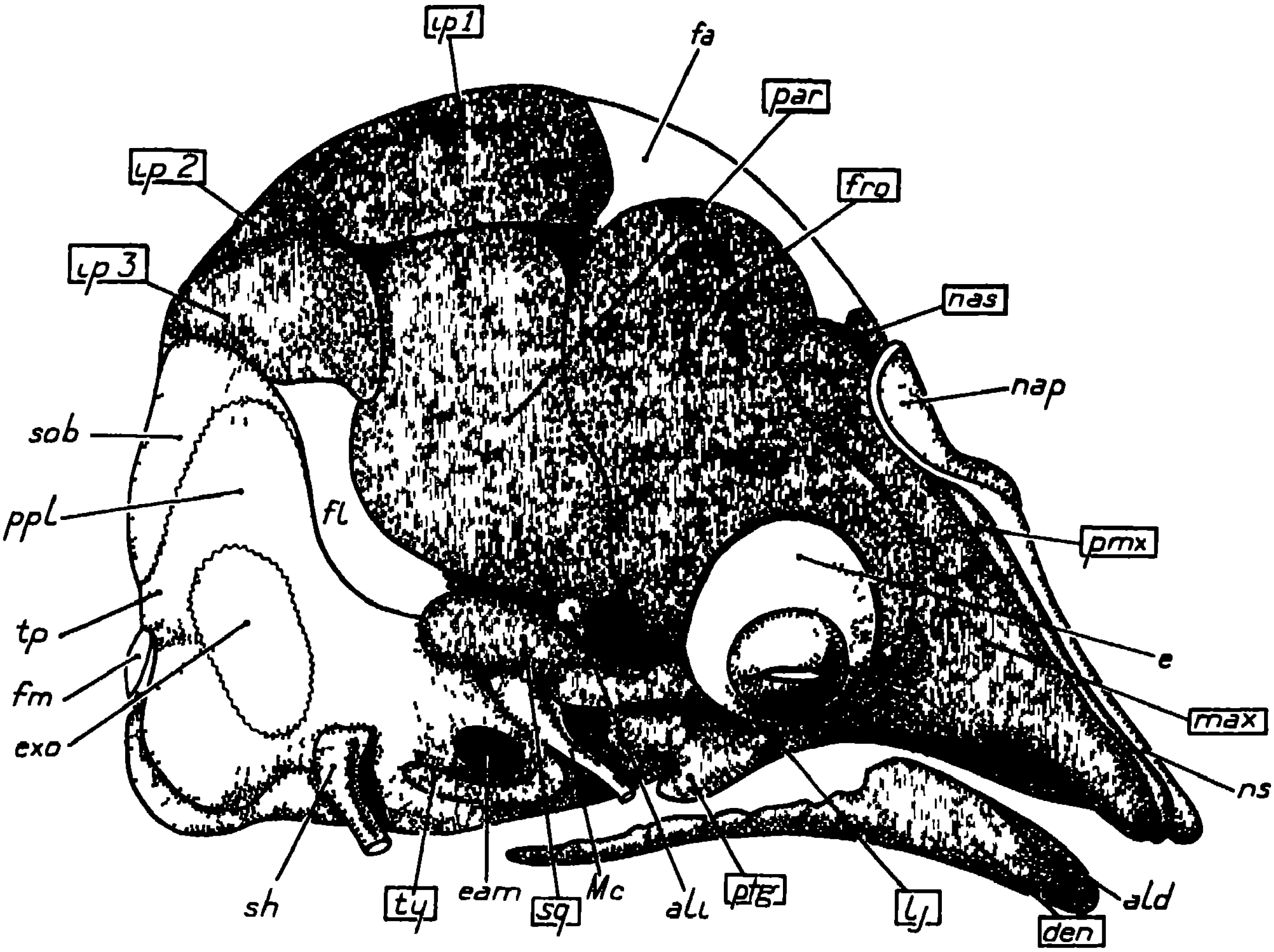

FIGURE 14 Foetus B Lateral view of the dissected skull Meckel's cartilage and the stylo-hyale have been cut short A portion of the dentary has been drawn to indicate its position and down-turned symphysial end (Magn ×4)

The lachrymo-jugals (*lj*) are still pressed in and under the eye Posteriorly each almost touches the post-orbital process of the frontal

The squamosals (*sq*) have developed glenoid surfaces for the condyles of the dentary

The tympanics (*ty*) are closing the gap in the crescent as they broaden

The palatines (*pab*) approach one another but do not quite meet on the palate The pterygoids (*ptg*) show little further development

The vomer (*vb*) is less exposed owing to the growth of the maxillae and palatines

The dentaries (*den*) have shaped themselves and show a curved alveolar groove on the antero-dorsal border of each

The chief bony developments at this stage are

The growth of the premaxillae and maxillae in relation to the extension of the nasal septum

The partial covering of the vomer by palatal processes of the maxillae and the palatines
The enlargement of the alveolar groove in each dentary

DISCUSSION AND CONCLUSIONS

Characters of the order, suborder and family

The foetal narwhal exhibits many of the characteristics of the adult animal Externally the blow-hole, small, downwardly directed eyeball, minute external auditory meatus without a pinna, paddle-like fore-limbs, tail fluke and external genitalia are sufficiently well developed to distinguish not only the order and sub-order to which the two foetuses belong, but their genus and sex It is unfortunate that no younger specimens are available and also that no accurate estimate of the age of these two foetuses could be made, owing to the scarcity of the material and the almost entire absence of data regarding the duration of the gestation period

If the specimen in the American Museum of Natural History, measuring 225 mm is between three and four months old, as has been suggested, then these two specimens are considerably younger, and are the youngest yet recorded

Internally the restriction of the hair germs to the region of the mouth and the continuous sheet of blubber beneath the skin are features of the Cetacea, as also are the rounded skull, with depressed front and high, domed brain case, the weak zygomatic arch and mandible, laterally restricted frontals and parietals, and greatly developed supra-occipital and inter-parietal

The narwhal agrees with other members of the Odontoceti in the presence of teeth Like them it has small nasal bones not roofing in the nasal passages The olfactory lobes of the brain and the olfactory nerves have disappeared with degeneration of the olfactory organ, and turbinal bones are absent The maxilla overlaps the frontal, and both the latter and the parietal are pushed back on the skull, neither reaching the vertex The lachrymal is fused with the jugal and there is no naso-lachrymal canal The auditory capsule has rotated to a transverse position, with a very large antero-ventral cochlear portion and small postero-dorsal canalicular portion The result is that the internal auditory meatus faces dorsalwards, the fenestra ovalis antero-ventrally The flat rami of the mandible unite in a mental symphysis

In the Monodontidae the head is rounded and not prolonged forwards as a rostrum, though in the adult the skull is elongated anterior to the blow-hole by the extension of the premaxilla and maxilla, carrying with them the nasal septum, bearing the tusk or tusks, but this is largely hidden by blubber The adult has no hair, but the foetus exhibits seven pairs of hair germs on the lower jaw The dentition is reduced, in the male only one tooth or a pair of teeth being visible in the form of a straight, tapering tusk usually on the left side, or more rarely a pair of tusks This tusk may attain a length of more than half that of the body (9 ft in a 15 ft body), and is spirally coiled sinistrally The tooth on the right side may remain concealed, or it may also form a sinistrally coiled tusk In the female, two short tusks may be formed, or one or none It has been known for the past century that two pairs of teeth are formed in the upper jaw, the second pair aborting or falling out The lower jaw does not produce teeth The foetus, however, exhibits dental papillae, equal on both sides, for both the above pairs of teeth, and in addition four small dental papillae on a diminishing dental lamina on each side, the whole of the tooth band lying in a groove in the maxilla On the lower jaw the foetus shows traces of two pairs, with the corresponding continuous alveolar groove, in the short, down-turned dentary

Comparison of foetal and adult narwhal skulls (figure 15)

The skulls from foetal narwhals A and B were compared with a young adult skull in the British Museum (Natural History)

	A	B	young adult
length of pre-orbital region to total length	1 3 75	1 3 2	1 2 5
position of blow-hole	antorbital	antorbital	postorbital
length of brain case to total length	1 1 05	1 1 4	1 3 9
height to length	1 1	1 1 4	1 1 65

Although therefore the narwhal characteristics are pronounced in the foetal stage, the proportions show a progressive change with age Briefly these involve an elongation of the cranial rostrum in order to carry the weight of the tusk, the pushing back of the blow-hole to a post-orbital position and its elevation from an anterior to an antero-dorsal position, the shortening of the brain case relative to the total length of the skull, and a small relative increase in height, chiefly due to the development of the brain case floor in the exoccipital and squamosal regions The overlapping and telescoping of the bones, which are so marked a feature of adult cetaceans, has only just begun in the foetus The short, down-turned mandible lengthens relatively and straightens itself with age

Comparison with other members of the Odontoceti

The relationship of the narwhal to other members of the Odontoceti has been assessed chiefly on the external characters of the adult Earlier workers recognized four families Physeteridae, +Squalodontidae, Platanistidae and Delphinidae, but some of these have now been split up The Ziphiidae have been taken out of the Physeteridae, two new fossil families have been added (+Eurhinodelphidae and +Acrodelphidae), the Platanistidae remain untouched, and the Delphinidae have been divided into Monodontidae (for *Monodon* and *Delphinapterus*), Phocaenidae (for *Phocaena* and *Phocoenoides*) and Delphinidae for all the remainder This cuts across the older classification based on the length of the rostrum

The question then arises to which of these families is the Monodontidae most nearly related? In bodily contour it has resemblances to the Ziphiidae and some Platanistidae, in which the dorsal fin is reduced, the pectoral fin is small and broad, the neck vertebrae are free or nearly so, and the number of vertebrae is in the neighbourhood of fifty In the Ziphiidae the teeth are reduced to one or two in the lower jaw, the opposite of the condition in *Monodon* No information on the foetal stages of members of these families is available, and consequently relationships cannot be established

There remain the Delphinidae and Phocaenidae, and in these families investigation of both adult and foetal stages has been more extensive The foetal skull has been studied in *Phocaena* (de Burlet 1913*a*, Ridewood 1922, Slepzov 1940), *Globiocephala* (Schreiber 1916), *Lagenorhynchus* (de Burlet 1914*b*), *Delphinus* (Kesteven 1941, Slepzov 1940), and *Delphinapterus* (Slepzov 1940) Matthes (1921, 1923) has summarized the work done by observers up to those dates

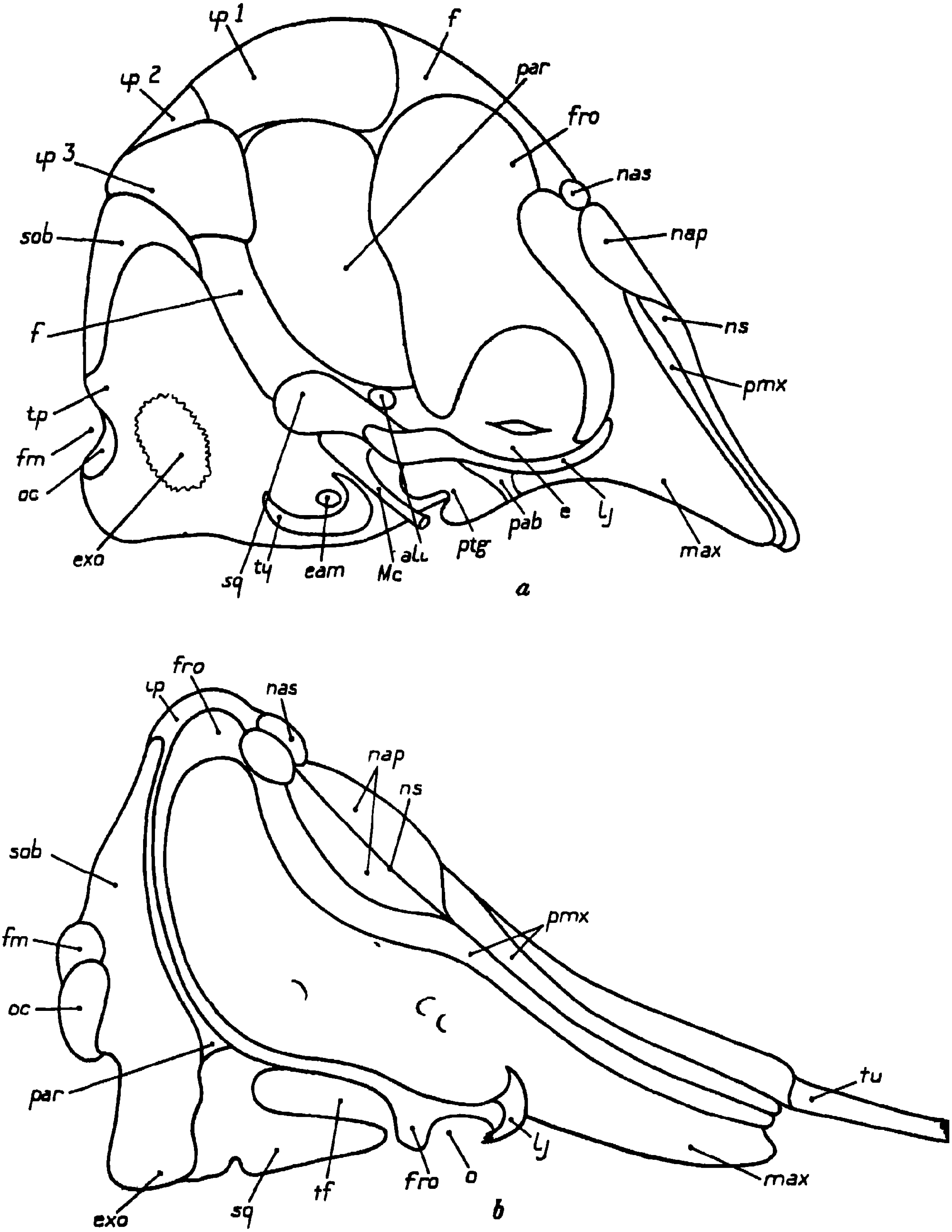

FIGURE 15 Comparison of foetal and adult skulls. The skulls have been drawn to the same length of base, and in lateral view *a*, Foetus B (Magn × 4) *b*, Young adult, from a specimen in the Natural History Museum, South Kensington The lachrymo-jugal and the tusk are broken off (Magn × ½)

The members of both families have a well developed dorsal fin, long, narrow paddles, numerous teeth on both jaws, a high number of vertebrae, and considerable fusion of the cervical vertebrae. With none of these characters does the narwhal agree. Despite these common characters, however, the foetal skulls fall into two groups:

(1) *Phocaena*, *Delphinus* and *Lagenorhynchus*.

(2) *Monodon*, *Delphinapterus* and *Globiocephala*.

In the first group the nasal region is not markedly reduced, both anterior and posterior paraseptal cartilages being represented, and in *Phocaena* a lamina transversalis posterior, and foramina cribrosa. *Delphinus* has olfactory nerves. *Lagenorhynchus* exhibits a sphenethmoid commissure, though in de Burlet's specimen this was present on the left side only. *Phocaena* possesses the posterior portion of the sphenethmoid—orbital—parietal band in the orbitoparietal commissure.

In the second group little is known of *Delphinapterus*, but *Monodon* and *Globiocephala* have the following characters in common. The chondrocranium is short and wide, with a flat floor, without a dorsum sellae. The cranial rostrum is also short. The nasal region is incomplete posteriorly, the posterior paraseptal cartilages and lamina transversalis posterior are present but reduced in *Globiocephala*, and absent in *Monodon*. The lamina orbito-nasalis is broad and flattened, and the foramen olfactorium advehens forms a longitudinal slit on either side of the narrow nasal septum. Cribriform plate, olfactory lobes and nerves are absent. Meckel's cartilages are strikingly similar, exhibiting a peculiar twist and curvature, with partial ossification in the early stages. *Globiocephala*, however, retains the orbitoparietal commissure, while *Monodon* has only a vestige of it on one side. The spina mesethmoidalis is absent in *Globiocephala*, and present in *Monodon*. But the general form of the chondrocranium in these two animals is very similar. One difference which links *Globiocephala* with the Delphinidae and Phocaenidae is the presence of a true alicochlear commissure between the lamina supracochlearis and the auditory capsule. Kukenthal (1908) also grouped these three whales, because of the similar extent of the asymmetry of the skull which they exhibit.

Comparison with the Mystacoceti

Knowledge of the foetal stages of members of the whalebone whales is confined to the genera *Balaenoptera* (de Burlet 1914*a*, Schulte 1916, Walmsley 1938) and *Megaptera* (Honigmann 1917, Ridewood 1922). It is therefore somewhat difficult to compare the two groups, especially as the Mystacoceti exhibit considerable variation in the chondrocranium and osteocranium even among species of the same genus. The two sub-orders possess certain common peculiarities, such as the flat broad skull base without dorsum sellae, the spina mesethmoidalis, lamina supracochlearis and alicochlear commissure, basi-cochlear fissure, rotation of the auditory capsule and its depressed position beneath the basal plate, large cochlea with 1⅛ to 2 turns—these characters are not collectively found in other orders of mammals. But in the Mystacoceti the nasal capsule is less reduced than in the Odontoceti, so that a completely ringed, though short, capsule is present, with a double blow-hole, a cribriform plate, turbinal cartilages and sphenethmoid commissures. The hypoglossal foramen is variable. Sometimes it is present on both sides, on one side, or it may be absent altogether, so that the nerve will leave by the jugular foramen. Equally variable is the interparietal bone, described by Ridewood (1922) as large in *Balaenoptera borealis*, small or absent in *B musculus* This requires further investigation

It has been stated by palaeontologists that the Mystacoceti are younger geologically than the Odontoceti Yet embryology shows that the specialized distinctive features of the whales appear earlier in development in the Mystacoceti It is perhaps difficult in the present state of our knowledge to reconcile these two statements, which might be modified if more material were available for study Until we can investigate a greater range of fossil whales and earlier foetal specimens of modern genera, we can place little reliance on conclusions drawn from so few specimens

It is possible that the two suborders are diphyletic and not very closely related

Comparison with other orders of mammals

If the whales are diphyletic they were probably derived, as Honigmann (1917) suggested, from carnivorous Eutherian ancestors But how those ancestors were related to other mammalian orders we do not know, and specialized types such as the modern whales do not give us any help Apparent resemblances with the Sirenia are probably due to convergent adaptations to an aquatic habit

Slepzov (1940) claims a very early ancestry for the Odontoceti, with persistence of reptilian features in the skull He states that in the foetus of *Phocaena* the parietal is a median bone which has been wrongly interpreted by zoologists as the interparietal The paired bone they call the parietal is to him the postfrontal, the paired portion of the interparietal is the tabular, and the posterior median interparietal retains its own name Since the Insectivora, one of the most primitive orders of Eutherian mammals, have no postfrontals, Slepzov considers that the Odontoceti are older than the Insectivora and represent a very ancient group There are two objections to this theory First the postfrontal bone of reptiles and amphibia had access to the wall of the orbit, which Slepzov's postfrontal has not, and secondly there is no ground for assuming a median *origin* for the parietal bone in Eutherian mammals With regard to the tabular, this pair of bones has been identified in *Chrysochloris* (Broom 1916, Forster Cooper 1928), *Phoca* (Watson, verbal communication 1916)and as long ago as 1885 W K Parker noted a pair of postparietal bones in *Microgale* which he called supra-temporals, but which we should now call tabulars The tabular has relations with the supra-occipital, parietal, ex-occipital and periotic, the last of which it partly covers In reptiles the two bones are separated by the dermal supra-occipital, now identified as a paired interparietal (von Huene 1912) The tabulars move forwards out of the occipital ring in mammals, probably owing to the disappearance of the supra-temporals, but in no case do they make contact with one another in the mid-dorsal line In other words they are in the longitudinal plane of the ex-occipitals Now in foetus A the membrane bone, called above interparietal, ossifies from four centres, two median, one behind the other, and a pair alongside the posterior median bone, which is slightly sunken In foetus B the pair of bones meet on the summit of the head mid-dorsally Because of this dorsal position there seems little justification for claiming them to be the tabular bones, and accordingly all four bones have been named interparietal In Slepzov's *Phocaena*, the head of which was about half the length of the head of narwhal foetus A, the bones labelled tabulars were lateral in position It would be interesting to ascertain whether in older porpoises these lateral elements grew over towards the mid-dorsal line, as they do in the narwhal If they do, they are probably not tabulars

SUMMARY

1 The heads of two narwhal foetuses from Greenland were investigated for the structure of the chondrocranium, early osteocranium and the membranous labyrinth Until this work was undertaken, nothing was known of the development of the skull in the narwhal

2 Specimen A (137 mm long) was sectioned transversely and models were prepared by the wax plate method of the chondrocranium, the complete skull, the brain and the membranous labyrinth The skull of specimen B (150 mm) was exposed by dissection, and cut in sagittal section

3 Although so young, the foetuses exhibited the generic characters of the narwhal, and their sex was determinable, both being females The chief external difference was the position of the blow-hole, which was directed forwards in the smaller foetus, antero-dorsally in the older one

4 One pair of hypoglossal foramina and large inflated paracondylar processes are present

5 The auditory capsule, free in adult Cetacea, is moored to the chondrocranium by true and lateral prefacial, orbito-capsular, postfacial and basivestibular commissures There is no alicochlear commissural attachment, or other connexion with the basal plate, and the capsule is sunk below the level of the latter, the lamina supracochlearis extending like a shelf over it The basicochlear fissure is continuous and well defined The complete isolation of the auditory capsule mesially confirms the view that the cochlear portion of the capsule is a true part of it and is not a derivative of the parachordal plate

6 The ala temporalis is imperforate, the alisphenoid is a cartilage bone

7 There is no dorsum sellae Preoptic and metoptic roots of the orbital cartilage and an ala hypochiasmatica on the anterior border of the foramen are present

8 There is no trace of a sphenethmoid commissure

9 The lamina orbitonasalis is broad and flat, as in *Globiocephala*, and the foramen olfactorium advehens forms a longitudinal slit on either side of the narrowed nasal septum

10 A spina mesethmoidalis is present

11 The nasal capsule is greatly reduced, the tectum and paries nasi are weak There is a lamina transversalis anterior but not posterior No posterior paraseptal cartilage A remnant of the cartilago naso-palatini lies close against the nasal septum, but there is no trace of Jacobson's organ The only remnant of the posterior portion of the capsule is the reflected edge of the lamina orbitonasalis

12 Meckel's cartilages are slender and twisted, and resemble in shape those of *Globiocephala*

13 The tegmen tympani and crista parotica are well developed

14 There is some continuity between the malleus and the incus In sections the stapes exhibits a small hole between the crura, but this is not visible externally

15 A pre-articular (goniale of Gaupp) is present

16 The interparietal, ossifying from four centres, forms the main part of the roof of the skull No evidence that it represents more than a compound interparietal can be adduced

17 There is no separate lachrymal

18 The upper jaw has two teeth on each side and dental papillae for four others, all in an alveolar groove in the maxilla The lower jaw shows dental papillae for two teeth on each side and a well developed alveolar groove in each dentary These teeth are never cut

19 Seven hair papillae are present on each side of the lower jaw These also are vestiges The adult narwhal has no hairs

20 The study of the foetal skull leads to the conclusion that the Monodontidae are related to the Delphinidae more closely than to the Phocaenidae, and approach the Delphinidae through *Globiocephala*

I am indebted to all who have so generously given me their help, advice and criticism Professor O'Donoghue has given me every facility for work in his department Dr F C Fraser allowed me to sketch young and adult narwhal skulls in the Natural History Museum and lent me X-ray negatives of foetuses in the possession of the Museum Dr Keith Richardson cut the sections in celloidin, and Mr F C Padley built up the models and photographed them My special thanks are due to Professor G R de Beer, who discussed many points with me His extensive knowledge of the development of the vertebrate skull has been of the greatest service to me

To the Research Board of the University of Reading I express my gratitude for grants towards the costs of the equipment and the illustrations, the latter so ably executed by Miss E C Humphreys

Reference Letters

(Wherever possible, the reference letters are the same as those used by Professor de Beer in *The Vertebrate Skull*)

a, auditory capsule
ah, ala hypochiasmatica
ald, alveolar groove in dentary bone
ali, alisphenoid bone
alm 1, alveolus in maxilla for first tooth
alm 2, alveolus in maxilla for second tooth
amp, ampulla
at, ala temporalis

b, buccal cavity
bcf, basicochlear fissure
bh, basihyale
bl, blubber
bo, basioccipital bone
bvc, basivestibular commissure

c, isolated cartilage near blow-hole
cav, anterior vertical semicircular canal
cb, crus breve of incus
cbm, cerebellum
cc, canalicular part of auditory capsule
cdn, cartilago ductus nasopalatini

ce, cerebral hemisphere
ch, horizontal semicircular canal
chp, choroid plexus
cl, crus longum of incus
coc, cochlear part of auditory capsule
coch, cochlea
copv, vestige of orbito-parietal commissure
cpv, posterior vertical semicircular canal
cr, crus commune
cre, canalis reuniens between saccule and cochlea
crp, crista parotica

d 1, first or tusk-forming tooth
d 2, second tooth
den, dentary bone
dll, dental lamina of lower jaw
dlu, dental lamina of upper jaw
dp 3, third dental papilla
dp 6, sixth dental papilla

e, eyeball
eam, external auditory meatus

ec, epiglottal cartilage
Et, Eustachian tube
exo, exoccipital bone

f, fontanelle
fa, anterior fontanelle
fac, foramen acusticum internum
fc, carotid foramen
fen, foramen endolymphaticum
ff, foramen for facial nerve
fh, hypophysial foramen
fj, jugular foramen
fl, lateral fontanelle
flm, foramen lacerum medium
fm, foramen magnum
fo, optic foramen
fol, foramen olfactorium advehens
fp, foramen perilymphaticum
fro, frontal bone
fsm, stylomastoid foramen

Gg, Gasserian ganglion

h, hypophysis
hf, hypoglossal foramen
hg, hair germ

i, incus
ip 1, median anterior interparietal bone
ip 2, median posterior interparietal bone
ip 3 and 4, paired lateral interparietal bones

lj, lachrymo-jugal bone
lon, lamina orbitonasalis
lsu, lamina supracochlearis
lta, lamina transversalis anterior

m, malleus
max, maxillary bone
Mc, Meckel's cartilage
med, medulla oblongata
mm, manubrium of malleus
mr, metoptic root of orbital cartilage
mu, muscle

n, notochord
nap, nasal aperture
nas, nasal bone
nph, naso-pharynx
ns, nasal septum
nt, nasal tube

o, orbit
oc, occipital condyle
occ, orbito-capsular commissure
onf, orbito-nasal fissure
orc, orbital cartilage
ors, orbitosphenoid bone

p, parachordal or basal plate
pab, palatine bone
pal, processus alaris
par, parietal bone
pcc, parieto-capsular commissure
pcp, paracondylar process
pl, pars lateralis of parietal plate
pmx, premaxillary bone
pns, paries nasi
ppl, parietal plate
pps, palato-pharyngeus sphincter
pr, preoptic root of orbital cartilage
ps, paraseptal cartilage
ptg, pterygoid bone

s, stapes
sac, saccule
sen, saccus endolymphaticus
sf, sphenoidal fissure
sh, stylohyoid cartilage
sme, spina mesethmoidalis
sob, supra-occipital bone
sp c m, sphincter colli muscle
sq, squamosal bone

t, trabecular plate
tf, temporal fossa
thy, thyrohyoideus muscle
tn, tectum nasi
tp, tectum posterius
tty, tegmen tympani
tu, tusk
ty, tympanic bone
tym, tympanic membrane

utr, utricle

vb, vomer bone

V *cm*, mental branch of trigeminal nerve
V *cd*, inferior dental branch of trigeminal nerve
V *cmh*, mylohyoid branch of trigeminal nerve
VII, facial nerve

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ALVEOLAR EPITHELIUM IN RELATION TO GROWTH OF THE LUNG

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(*Communicated by G. R. Cameron, F.R.S.—Received* 22 *February* 1950)

[Plate 1]

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In the majority of organs which possess a lumen an epithelium is interposed between the parenchyma of the organ and the luminal space. Usually this epithelium lies upon a well-defined layer of fine reticulum fibres which constitutes the basement membrane. The developing lung of the embryo rabbit is no exception to this general rule, at any rate until the 24th day of embryonic life, when the complicated branching lumen is everywhere lined by tall, columnar epithelium supported by a reticular basement membrane. But histological examination of the lung of the adult rabbit shows no sign of epithelium or basement membrane. Indeed, the surface structure of the alveoli of the adult mammalian lung is one of the oldest of the unsolved problems in histology.

A detailed study by several methods of investigation of the stages intervening between the embryo and adult lung shows that the luminal epithelium ceases to be visible after the 26th day of the 32-day gestation period. Before the 26th day, the total volume of epithelium increases but is unaccompanied by any evidence of cell division. Cell rupture is therefore imminent, and its results become apparent between the 24th and 26th days when degenerate nuclei are extruded into the distal part of the respiratory lumen from ruptured cell envelopes. The healthy epithelium of the more

Vol. 235. B. 622. (Price 13s. 6d.) 5 [Published 2 November 1950

proximal parts of the lumen persists as bronchiolar epithelium, in which quantitative evidence of normal cell division is found

These facts explain the difficulty in interpreting the picture of cell outlines which is seen when silver nitrate impregnates the cement lines between epithelial cells In the earlier days of embryonic life the impregnated cell outlines reveal the regular meshwork characteristic of a complete epithelium In the adult lung no such clear and regular picture is seen, and a close study of the intervening stages discloses that this irregularity of cell outlines starts at the 24th day and progresses with the degenerative changes in the epithelium and extrusion of nuclei When the lung starts to breathe such traces of impregnated epithelium as were present at term finally disappear In the adult rabbit, counts of nuclei in the alveolar septa show that there are not enough cells to do more than invest the capillary plexus and to provide nuclei for a few alveolar phagocytes Moreover, a method of investigation whereby the structure of the alveolar septum may be dissociated fails to reveal any trace of lining epithelium On histological grounds, therefore, the presence of an alveolar epithelium in the lung of the adult rabbit seems to be ruled out

Criticism can, however, be levelled against this conclusion on the grounds of lung growth It has been said that the presence of alveolar epithelium is required to account for further subdivision of the lung lumen during both pre- and post-natal life New evidence is given in the second part of this investigation which suggests that the complexity of subdivision of the lung lumen is determined by purely physical factors It is shown that the inequality of growth rates of total lung volume and of volume of the interstitial tissues is the fundamental factor which determines the complexity of lung architecture

The latter is the result of subdivision of the lumen by a complicated system of septa The greater the number of septa, the more complex is the subdivision and the higher is the pitch of differentiation By measuring numbers of septa in terms of the internal surface area of the lumen, a method has been found for quantitative estimation of differentiation A linear relation is found to exist between this estimate of differentiation on the one hand and the ratio of total lung volume to interstitial volume on the other

The values of this ratio increase throughout embryonic life Growth of interstitial tissue does not therefore keep pace with growth of total lung volume The deficit in terms of volume is made good by the increasing volume of the lumen, but there is another deficit For if interstitial tissue does not grow as rapidly as lung volume, then elastic fibres may be expected not to grow as rapidly If this is so (and it is the heart of the problem), they will stretch as the lung expands with growth, and the ratio of total lung volume to interstitial volume will be a measure of the stretch to which elastic fibres are subjected in the growing lung A linear relation is found between this ratio and numbers of septa, each of which contains a bundle of elastic fibres in its free edge It is this linear relation which suggests a causal relationship between tension and the structural complexity of lung architecture

Support for this view in lungs at term and during the early stages of post-natal life is given by the results of artificial distension The plan of the 5-day lung, the complexity of whose structure is much greater than that at term, can be reproduced by artificial distension of the dead lung at term Hence there can be no question of any vital processes of growth nor of epithelial activity Distension alters the lung architecture by altering fibre tension, especially the tension of elastic fibres In the living lung, it is very probable that active contraction of plain muscle in the mouths of alveolar ducts and their main subdivisions is also involved The fact that the structural results of respiration and 5 days' growth *in vivo* can be so completely reproduced by artificial distension, as it were *in vitro*, is good reason to believe that subdivision of the respiratory lumen in both cases depends upon the same factor, the tension in elastic fibres

PART 1 ALVEOLAR EPITHELIUM IN THE RABBIT'S LUNG

INTRODUCTION

One of the unsolved problems of lung structure is concerned with the existence of an epithelium covering the alveoli Epithelium is a continuous sheet of cells separated from the underlying tissues by a basement membrane This criterion is obeyed up to certain stages in the developing lung of the mammalian embryo In the embryo lung, the epithelium above and the capillary bed below lie in close apposition to the basement membrane So much is admitted by all observers In the adult lung, ordinary staining methods fail to reveal an epithelium The stages intervening between the clearly marked epithelium of the foetus and the obscure surface structure of the adult alveolus has not received thorough investigation

In this present work a detailed histological description of the life history of epithelium, basement membrane and capillary bed is given, and the limits of the basement membrane and the structure and extent of the capillary bed have been defined as accurately as possible The resulting picture of lung structure was encouragingly self-consistent and contained significant features which pointed unmistakably in the same direction Nevertheless, many obscurities remained, due largely to ignorance concerning the facts of lung growth as a whole This aspect has been studied and has corroborated and amplified understanding of the results from histological investigation The evidence from both sources favours the view that alveolar epithelium does not exist in at least one adult mammalian species

METHODS

The numbers of rabbit embryos used in the histological section are shown in table 1 A series of human embryos, whose fertilization ages were calculated from menstrual age, is shown in table 2

TABLE 1 SERIES OF RABBIT EMBRYOS

day	numbers of rabbit embryos	fixation *in situ* by perfusion
18	3	—
21	4	—
22	6	—
24	6	—
26	6	—
27	4	—
28	6	3
30	6	2
31 (birth)	6	3
1 hr after birth	2	2
4 hr after birth	2	2
6 hr after birth	4	4
24 hr after birth	6	3
2 days after birth	6	3
5 days after birth	3	3
10 days after birth	3	3

TABLE 2 SERIES OF HUMAN EMBRYOS

fertilization age (days)	fertilization age (days)
50	150
53	157
80	164
91	166
98	168
109	170
112	172
126	180
134	217
137	231
146	266

Methods of fixation

Depending upon the age of the rabbit embryo, two routine methods have been employed In the case of embryos younger than the 28-day and some embryos between the 28th and 31st days, after killing by strangling, the lungs were fixed for 48 hr in 10 % formol saline after opening the thorax The whole thorax was dehydrated in 70 % alcohol for 48 hr, when the lungs were carefully removed and their edges trimmed before further slow dehydration in 90 % and absolute alcohol After clearing in chloroform the whole lung was embedded in paraffin at 56° C Sections were cut at 5, 15, 30μ and very often at 50 or 70μ

In the case of some foetuses between the 28th and 31st days and all lungs which had breathed, the foetus was killed by intraperitoneal injection of nembutal The abdomen was opened and the posterior abdominal wall exposed 3 ml of 10 % formol saline were injected very slowly into the inferior vena cava and the whole embryo was then immersed in 10 % formol saline After 48 hr fixation, the thorax was opened for the first time and the lungs removed Subsequent treatment was the same as in the first group In the case of foetuses whose lungs are fluid-filled *in utero*, no significant difference attributable to fixation was found in the histological examination of both groups In the group of air-filled lungs fixation *in situ* by perfusion is essential

Staining methods

Ehrlich's acid haematoxylin and eosin Heidenhain's iron haematoxylin, differentiation to varying depths being carried out on three parallel sections Van Gieson's stain Shaw Dunn's modification of Mallory's stain for connective tissue Weigert's elastic stain Orcein Laidlaw's method for reticulum

Lungs injected to show the capillary bed

The numbers of animals are shown in table 3

TABLE 3 INJECTED LUNGS IN RABBIT EMBRYOS

day	number injected	number injected and one lung distended
23	2	—
24	2	—
25	2	—
26	3	—
27	2	—
28	3	—
31 (birth)	—	4
1 hr after birth	—	2
4 hr after birth	—	2
6 hr after birth	—	2
1 day after birth	—	4
2 days after birth	—	4

Method of injecting the blood vessels of the lung

This is most easily accomplished in deeply anaesthetized foetuses when respiration is failing but before death If death has occurred most of the injection passes into the systemic circulation without entering the lungs If gasping is taking place, the lungs fill with the injection mass and the foetus may be killed at once by strangling The injection is best made into the inferior vena cava and without opening the thorax In foetuses which have breathed or in the adult, the results are incomparably better when injection is made with the thorax unopened If it should be necessary to distend the lungs, choice between air or formol saline will depend upon whether the lungs are aerated or not It is a mistake to inject air into lungs which have not breathed or have only gasped, since uniform distension will seldom be obtained owing to the presence of fluid which is normally present in the lumen of embryo lungs

Choice and preparation of the injection mass

If merely an injection of the capillary bed is required, India ink diluted 8 times with a solution of 0 5 % protein (dried human serum) in normal saline can be used Weaker dilutions sometimes permit of a nuclear counterstain When good nuclear counterstaining is essential, the transparent carmine-gelatin mass must be used It is most easily prepared as follows

Allow 20 g of gelatin to swell in 400 ml of distilled water and warm to 60° C Dissolve 5 g carmine in strong ammonia and add to the gelatin Filter while warm Place the filtrate in a pH meter and add acetic acid till the voltage is equivalent to pH 7 2 Add a crystal of thymol It is of assistance to wash out the blood by preliminary perfusion with saline on the acid side of neutrality, to prevent solution of the colloidal carmine After completing the injection, the embryo should be placed in ice-cold formalin and left there for 48 hr In the case of an adult rabbit, after completion of the injection, ice-cold formalin can be injected into the trachea in sufficient quantity to distend the lungs to their normal size Blocks are cut after partial dehydration in 90 % alcohol and are dehydrated and embedded in paraffin wax in the usual way

Impregnation by silver nitrate

For impregnation of epithelium or vascular endothelium, I have used 0 2 % silver nitrate in distilled water I can find no advantage in the several modifications A preliminary rapid perfusion by 2 % potassium nitrate (suggested by Carleton 1938) removes excess chlorides and reduces interference by precipitates If the silver solution is injected into the trachea, preliminary perfusion of the pulmonary artery by potassium nitrate can be used with advantage even if the lungs are fully aerated, if an impregnation of vascular endothelium is required, potassium nitrate is followed by silver nitrate in the pulmonary artery In spite of the intense vaso-constriction produced by silver nitrate, satisfactory impregnation of the capillary bed can generally be found in small areas of the lung

The lung is removed from the thorax and placed at once in 90 % alcohol in the dark Blocks are cut after hardening for 48 hr or longer and left in 90 % alcohol for a further period of 48 hr Dehydration is then proceeded with and the tissue is embedded in paraffin wax Sections are cut at 5, 50 and 100μ, taken to distilled water and placed in a mixture of equal parts of solutions A and B

solution A	
metol	30 g
potassium metabisulphite	30 g
sodium bromide	30 g
distilled water	1000 ml

solution B	
sodium hydroxide	50 g
distilled water	1000 ml

Impregnations can sometimes be improved by cautious use of 2 % potassium thiosulphate or by 0 5 % potassium ferricyanide, followed by thorough washing Its use should, however, be limited to removal of slight precipitate in good preparations intended for subsequent photography It is dangerous if used to improve bad preparations, and its routine use is likely to lead to results which are deceptive

A nuclear counterstain is possible where too much silver has not been deposited at the nucleus It is here that potassium ferricyanide is of great help to remove all impregnation from companion sections and thus to permit the use of any routine staining method

The routine study of impregnations has been made with a camera lucida and oil-immersion objective To draw a complicated system of lines is the best way to understand it Completely erroneous impressions arise unless differences of focal depth are observed before the lines are drawn Lines appearing to join may be shown to cross when an oil-immersion objective is used

HISTOGENESIS OF THE LUNG OF THE FOETAL RABBIT

General histological description

It will be convenient to describe the development of the foetal lung before considering certain aspects of this process in detail

Development of the lung of the foetal rabbit consists in repeated subdivision of the original paired tubes which are surrounded by vascular mesenchyme During the last week of development the branching lumen, which occupies about 20 % of total lung volume at the 21st day, has expanded to fill about 50 % at term The remaining portion consists of epithelium, connective tissue and blood vessels

At the 20th day the epithelium of the respiratory tubes is uniform, closely set, cylindrical and pseudo-stratified It lies on a well-defined basement membrane of reticulum fibres which contains small quantities of collagen and elastic in the larger tubes Outside the basement membrane is a cellular mesenchyme, rich in reticulum fibres and containing capillaries which are condensed to form a plexus around the respiratory tubes By the 22nd day, considerable elongation and subdivision of the tubes has occurred, and the larger tubes are lined by the same tall, columnar epithelium Distally the epithelium can be separated into two types the bronchiolar epithelium is cuboidal or low cylindrical, whilst in positions corresponding to the future alveolar ducts the epithelium is flatter and less closely set (figure 1) At the extreme tip of the tubes, the epithelium is cylindrical and pseudo-stratified Throughout, the basement membrane consists largely of reticulum with a fine deposit of elastic and collagen fibres

Distribution of reticulum fibres

By the 24th day, three condensations of reticulum are found between adjacent tubes (figure 2), of which the two outer layers form the narrow but densely woven basement membranes of the epithelium Between them is a third, less dense condensation, composed of thicker fibres of reticulum Two potential spaces are thus formed in the mesenchyme between adjacent tubes, and injected specimens show that these spaces are filled by the capillary plexus which surrounds each tube (figure 3) These plexuses are very profuse, their density being comparable with that of the capillary bed of the adult alveolus The plexuses have developed as separate vascular condensations around each tube since interconnexions between adjacent plexuses are not numerous The capillaries are of wide and somewhat variable diameter resembling sinusoids, and are closely apposed to the basement membranes

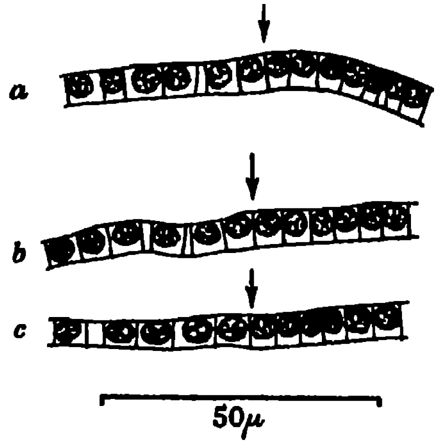


Figure 1 The arrow marks the change in character of epithelium at the distal limit of the bronchioles (on the right) *a*, 22nd, *b*, 23rd, *c*, 24th days

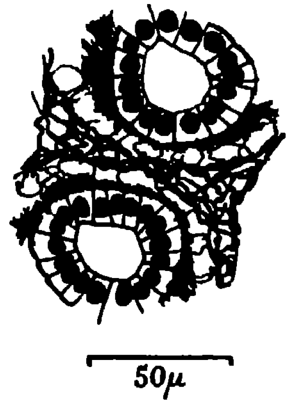


Figure 2 Reticulum condensations in intertubular septa Spaces containing few fibres are seen below the basement membranes for accommodation of the double capillary plexuses 22 days

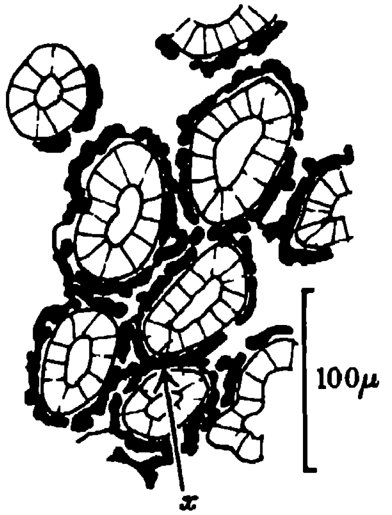


Figure 3 Double capillary plexuses in intertubular septa Early signs of fusion of the plexuses are seen at *x* 24 days

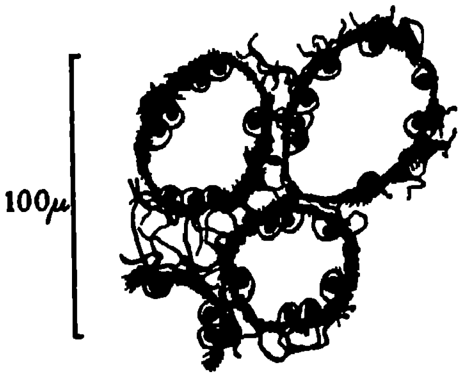


Figure 4 Reticulum condensations in intertubular septa at 25 days, for comparison with figure 2 Where fusion of double plexuses has occurred, one space crossed by reticulum fibres is found below the basement membranes for accommodation of the single capillary plexus

At the 23rd day, the terminal portions of many tubes have come to lie so closely to each other that the capillary plexuses surrounding them have fused to form a single plexus

Where such fusion has occurred, the single plexus is now confined by the two basement membranes, and is supported by the looser central condensation of reticulum (figure 4) Nowhere has the capillary plexus penetrated the basement membranes

Basement membranes

The structure of these basement membranes is best seen in thick sections where the full extent of the septum is lying flat, in the plane of the microscope stage They are formed by narrow, yet dense felt-works of fine reticulum fibres (figure 5) Thicker fibres join the loose reticulum condensation in the centre of the septum, but these are relatively few and serve to emphasize the individuality of the basement membranes The central condensation consists in thicker fibres threading their ways through the capillary mesh and thus forming the central support of the capillary wall

Figure 5 Basement membrane at 23 days Surface view

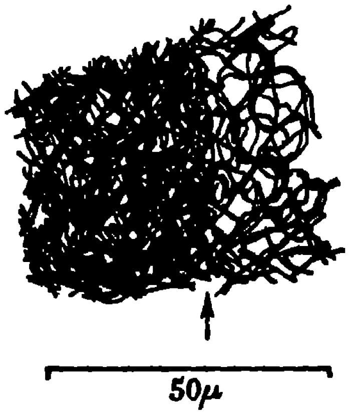


Figure 6 The arrow marks the termination of the basement membrane of the bronchiole (to the left) 26 days

Disappearance of basement membranes

By the 26th day the basement membranes extend no farther than the termination of cuboidal epithelium of the terminal bronchioles (figure 6) Distally, they exist as islands

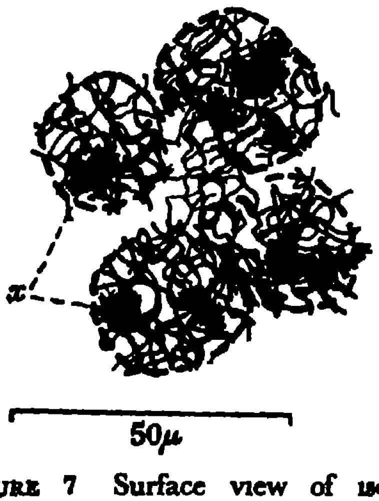


Figure 7 Surface view of isolated remains of the basement membrane (*x*) 26 days

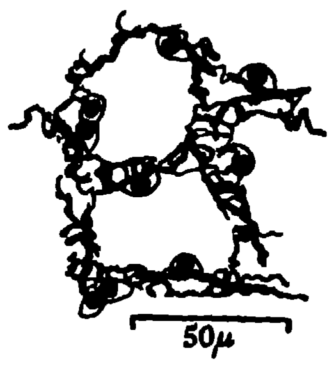


Figure 8 Reticulum condensations in intertubular septa The epithelium and basement membranes have disappeared 28 days

over small areas (figure 7) The continuity of these basement membranes has vanished, and this cannot be the effect of stretching or of separation of their constituent fibres since the quantities of reticulum which are involved are far too large By the 28th day all trace of the basement membranes has vanished (figure 8)

Epithelium, 23rd to 26th days

Tubes distal to the bronchioles are lined at the 23rd day by a complete cuboidal epithelium At the 24th day, a slight but definite change is found at the distal limit of the bronchioles which intensifies as the 26th day is reached (see figure 1) Many cells appear to be stretched, and of these several do not contain a nucleus Striking changes may be found in the remaining nuclei which are often much enlarged, palely staining or fragmented They may also be observed in all stages of extrusion from the ruptured cell envelope into the lumen of the tube (figure 9) In the remaining epithelial cells of the distal tubes (the future alveolar ducts) mitoses are rarely seen

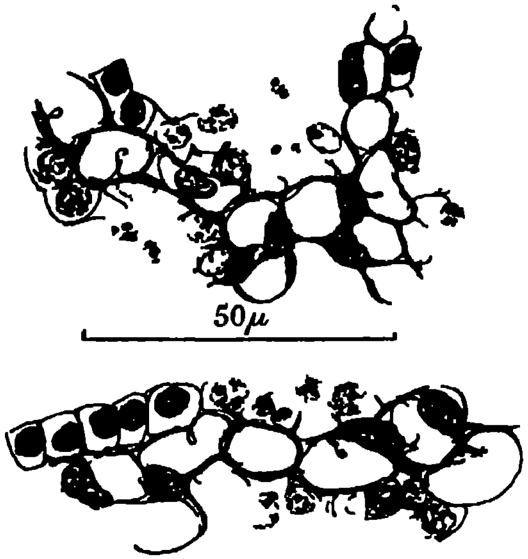


FIGURE 9 Degenerate epithelium of alveolar ducts showing extrusion of nuclei (24 to 26 days)

Desquamation of epithelium

Between the 24th and 26th days larger or smaller numbers of extruded nuclei can be found in the lumen of what have now become the alveolar ducts The nuclei, fragmented or pycnotic, may be associated with granular debris, sometimes the whole epithelial cell may be found Here and there the flattened or twisted endothelial nuclei of the capillaries are seen lying in direct contact with the lumen Earlier, a perfectly definite, complete and nucleated epithelium lying on a well-defined basement membrane has separated the capillary from the lumen Elsewhere the capillaries are separated only by the non-nucleated remains of the original epithelium, represented by the empty cell envelopes which by slight overlapping at their edges and their well-marked cell membranes somewhat resemble the horny layer of the skin Desquamation of these cell envelopes may sometimes be observed as minute disorganized laminae fraying off into the lumen, but extrusion of nuclei is more often found than is desquamation of the cell envelope

At the 24th to 26th day, in the terminal portions of the respiratory tubes and especially in those which abut against the pleura or against a bronchus or branch of the pulmonary artery, the epithelial island is still present and each cell is nucleated In the incomplete epithelium of the alveolar ducts, smaller isolated groups of cells may also be found

An injected specimen of the rabbit's lung at the 25th day does not support the view that there is any capillary proliferation between the epithelial cells In this species there is no evidence that desquamation of epithelium is either caused or accompanied by capillary proliferation

Alveolar epithelium in the human lung

The same sequence of events which has been described in the foetal rabbit has been found in man Though it is impossible to fix the lungs so rapidly (as is possible with the rabbit) as to avoid all possibility of autolysis, enough fresh human embryonic material exists to convince me that autolysis is not a serious matter in the series of embryos which have been studied

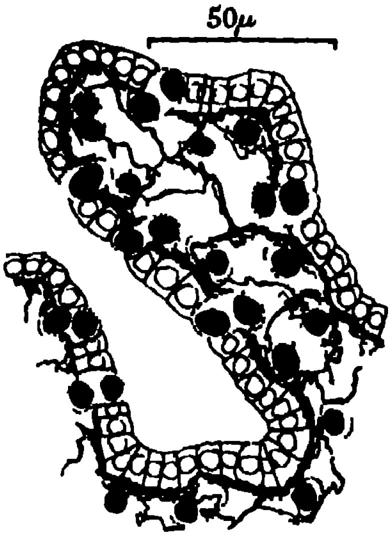


FIGURE 10 The basement membrane is deficient at the points where capillaries protrude between epithelial cells Black cells are erythrocytes in this and the following figures Human embryo, 100 days

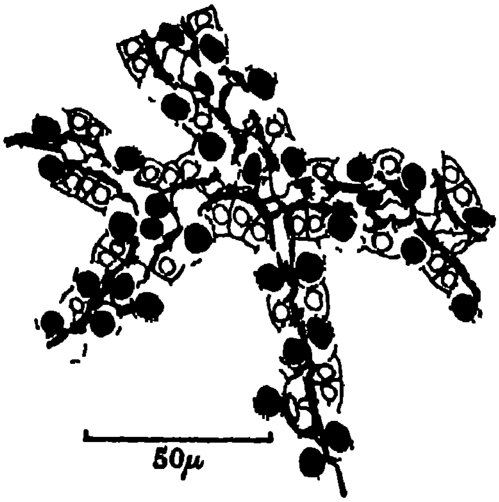


FIGURE 11 More advanced protrusion Considerable reduction of numbers of epithelial cells Human embryo, 146 days

In the rabbit the process of desquamation occurs between the 24th and 26th days and is completed on the 27th day In the human embryo, the earliest stages of the process can be recognized at the 110th day and are usually complete by the 170th day It is unlikely, however, that the process of desquamation lasts for so long in the development of one embryo Four stages of development can be described

Up to the 110th day The respiratory tubes are lined by a complete, tall-columnar epithelium which gradually becomes less tall It lies on a well-defined basement membrane of fine, closely woven fibrils of reticulum beneath which lies the capillary plexus and a few loose reticulum fibres in the central part of the septum

110th to 150th days The earliest signs of incomplete epithelium are seen as a result of the protrusion of capillaries between adjacent epithelial cells At these points the basement membrane is incomplete, and in surface view the defect appears as a small round hole of the diameter of a capillary By the 150th day numerous protruding capillaries may be found, and by coalescence the gaps in the basement membrane may become larger The appearance of the protruding capillaries is exactly that described by Barnard & Day (1937), who attributed it to proliferation of the capillary plexus

150th to 170th days Epithelium has disappeared from large tracts of the surface of the alveolar ducts, though it is still complete in their extreme tips Occasional epithelial cells, usually single but sometimes in groups, can be seen lying on the capillary plexus or extruding their nucleus into the lumen of the alveolar duct Retained nuclei may be swollen, pycnotic or fragmented The basement membrane no longer exists on the luminal surface of the capillary plexus except in the extremities of the respiratory tubes On the other hand, a narrow but definite condensation of reticulum fibres is now seen on the deep surface of the capillary plexus by which the plexus is separated from the central parts of the septum in which reticulum fibres are sparse The septum has thus come to consist of a central very loose network of reticulum which lies between two parallel, finely woven condensations of reticulum upon whose luminal surfaces the capillary plexuses are placed These plexuses appear to lie in direct contact with the respiratory lumen except for an occasional, retained epithelial cell

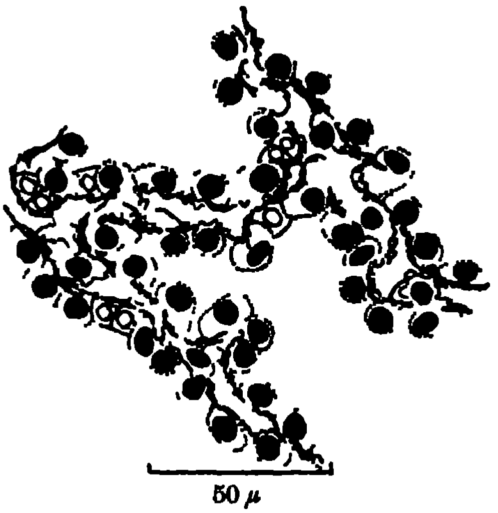


FIGURE 12 Reticulum has formed a new condensation on the deep surface of the capillary bed Epithelial cells are infrequent since most have desquamated 166 days

170th day to term Except at the extreme tips of the ducts, a continuous epithelium has vanished Two capillary plexuses lie on the surfaces of all septa which expose two surfaces to a lumen The plexuses lie on distinct condensations of reticulum between which sparse reticulum fibres run through the central parts of the septum In the early stages of this period, the central part of the septum is wide and the subcapillary condensations are consequently distinct As term is reached, more and more narrowing of the septa occurs until the subcapillary condensations have fused in many septa to become the single, central scaffold of reticulum which is characteristic of the post-natal and adult lung

The protrusion of capillaries between adjacent epithelial cells is undoubtedly very suggestive of the capillary 'proliferation' described by Barnard & Day (1937) Nothing of the sort is seen in the development of the rabbit What is known of the development of the pulmonary capillary bed does not support the view that proliferation by active growth takes place, and it may be that the more passive process of protrusion or bulging is associated with increased blood flow

The capillary plexus in man is separated from the epithelium by a well-marked basement membrane At the conclusion of the period of desquamation in man, an equally well-marked condensation of reticulum is seen on the deep surface of the capillary bed It would seem that the structures had changed their relative positions, but it is obvious that two meshworks (capillary plexus and basement membrane) cannot change their relative positions unless 50 % of both continue to lie in their original positions This, however, is not the case At least 80 % of the capillary plexus lies on the luminal surface of the reticulum condensation beneath it Few capillaries are to be found in the central part of the septum It would seem, therefore, that the original epithelial basement membrane had disappeared with the epithelium and that a new condensation had been formed on the deep surface of the capillary bed

The pulmonary lobule

Following desquamation of the alveolar epithelium of the embryo, the point of termination of bronchiolar epithelium can be supposed to represent the apex of the cone formed by the pulmonary lobule There is no other structure than this termination of bronchiolar epithelium which lies even roughly in the same relative position In lungs of a given age, the length of the alveolar ducts measured from the termination of bronchiolar epithelium to the lobular periphery is fairly uniform, but there is reason to believe that the distal termination of epithelium may not occupy the same relative position in lobules from lungs of different age groups Broman's (1923) observations in the cow and in man and Willson's (1928) observations in the mouse show that the number of bronchial divisions separating

TABLE 4 RELATION OF LUNG VOLUME TO LENGTH OF ALVEOLAR DUCTS

	length of alveolar ducts (μ)				lung volume (ml)	
age	measured	corrected for shrinkage (see table 11, part 2)	increase	(increase)^3	measured	calculated
Rabbit						
28 days (embryo)	210	225			1 1	
adult	800	800	3 54	44	45 75 [=]*	48 5
Man						
term	400	400			50	
adult	1500	1500	3 75	52 5	6000 [>]*	2625
Mouse						
term	190	190			0 03	
adult	400	400	2 1	9 3	0 7 [>]*	0 28

* The mouse and man possess respiratory bronchioles The rabbit does not, and in this species the cube of the increase by growth in alveolar duct length is a fair measure of increase in lung volume In the mouse and in man measured lung volume is almost three times as large as the calculated figure

the trachea from the alveolar ducts increases between birth and maturity Inexplicable on any other hypothesis, Bremer (1935) suggested that this increase in number of bronchial divisions is the result of a peripheral advance of bronchiolar epithelium, so that the alveolar ducts of the young are converted into the bronchioles of the adult

Data show that this manner of growth does not take place in the rabbit For the cube of the increase in length of alveolar ducts between two age groups multiplied by lung volume of the younger age group is found to be a fair measure of total lung volume (see table 4) In man and the mouse, on the other hand, such calculation is far below measured lung volume It is, indeed, probable that the manner of bronchiolization of alveolar ducts postulated by Bremer (1935) is limited to those species which possess respiratory bronchioles, and that it is absent in those species which do not possess them, as, for instance, the rabbit

DEVELOPMENT OF THE CAPILLARY BED

Foetal stage

The changes in arrangement of the reticulum condensations in the intertubular septa have been related to desquamation of epithelium and its basement membranes on the one hand and, on the other, to fusion of originally independent capillary plexuses

Throughout the foetal life of the rabbit, most of the intertubular septa (exposing two surfaces to adjacent lumina) contain two plexuses (Schultze 1871) These are developed as separate condensations around tubes In two characteristic situations the septa present only one surface to a lumen first in the subpleural extremities of tubes, and secondly in tubes whose extremities abut against an interstitial structure In these situations, the capillary bed is single, and this affords evidence that the primordial capillaries have condensed to form a plexus which envelops the developing lumen The capillary plexuses in these situations differ also from those throughout the largest part of the lung, in that their mesh is very much less complex Such is the case in the later stages of foetal life (figure 13) and also in the adult (figure 14), where the contrast in man has been illustrated by Miller (1937) Schultze (1871) appreciated that the larger mesh of subpleural alveoli was the result of persistence of a single plexus, the complexity elsewhere being the result of fusion of two originally separate plexuses Analogous conditions are found in the human foetus and in amphibian or reptilian lungs In the latter species, thick septa draw up two sheets of the capillary net, one on each side of the thick central stroma (Williams 1859), a condition which persists into their adult life

It is not difficult to imagine the stages leading to development of the relatively loose plexus found in subpleural alveoli It is a very different matter to imagine the development of so profuse a capillary net as that which invests the rabbit's lung at term Recognition of its development from fusion of two plexuses resolves the difficulty at least temporarily

Post-natal stage

The capillary bed would appear to be unfavourably placed for enlargement by the recognized method of formation of capillary loops The plexus is confined by adjacent alveolar surfaces and its mesh is narrower than the average diameter of its constituent capillaries It would appear, therefore, to be rigidly confined to the septum and to be of such an order of complexity that capillary proliferation is out of the question Yet it is clear that the onset of respiration must increase the respiratory surface and that the first month of life must involve a still greater increase How, therefore, does the capillary plexus accommodate itself to further growth of the lung?

At term, and indeed at all stages of the rabbit's life, the mesh size of the capillary bed is of two types The larger mesh is about half the complexity of the other, and is found in those alveolar septa which present only one surface to the respiratory lumen In these situations, below the pleura and abutting against interstitial structures, the capillary bed has been formed from one plexus In all other situations the capillary plexus is developed from two plexuses placed back to back

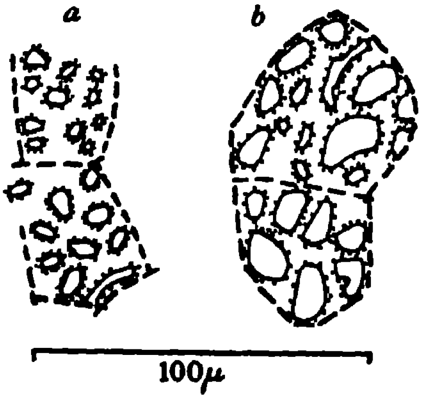


FIGURE 13 Comparison of mesh of capillary bed from normal alveolus (*a*) and subpleural alveolus (*b*) 1-day old rabbit

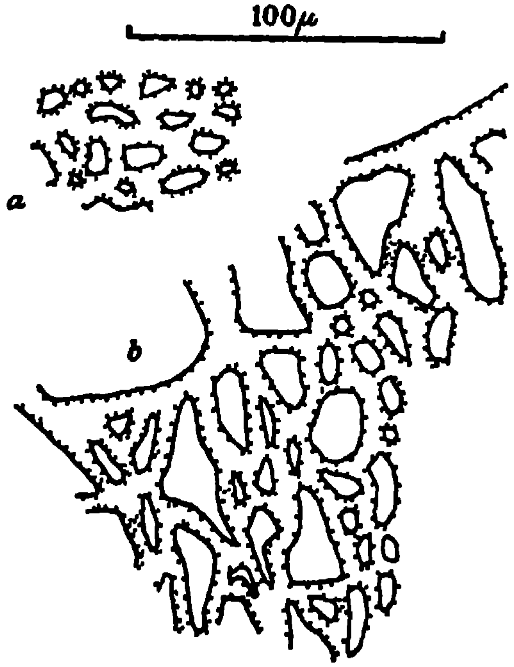


FIGURE 14 Comparison of mesh of capillary bed from normal alveolus (*a*) and subpleural alveolus (*b*) Adult rabbit

Post-natal growth of the lung will therefore have different effects on these plexuses In the plexuses of subpleural type, growth of the respiratory tree must enlarge the mesh of the plexus in all dimensions unless it is modified by capillary proliferation within the plexus itself In plexuses of normal type (exposing two surfaces to the lumina), growth and distension of the lumen must distend and enlarge each plexus, but it could also promote further and more complete fusion of the plexuses, so that by degrees their original double nature would become obliterated

Figure 15 shows that such local fusion actually takes place and that between birth and the 10th day of life the double character slowly disappears Even by 48 hr of life, the double character in many places could hardly be guessed without knowledge of the earlier state It can, however, be recognized in all stages of development of septa including the earliest, knob-like stage (figure 16)

Such fusion, amplifying that already noticed to occur in the embryo, provides for no more than a temporary increase in complexity It cannot provide for growth of the plexus when continual increase of surface area imposes still further demands on the capillary bed Unless the plexus stretches, some other method of reproducing itself must be found, and it would seem that only two ways exist by which this can be accomplished

By endothelial loops

This is the usual method by which a capillary bed enlarges Evidence can be found that it occurs in the lung where it appears to be limited to the largest intercapillary spaces of plexuses of the subpleural type Even here it seems to be relatively uncommon

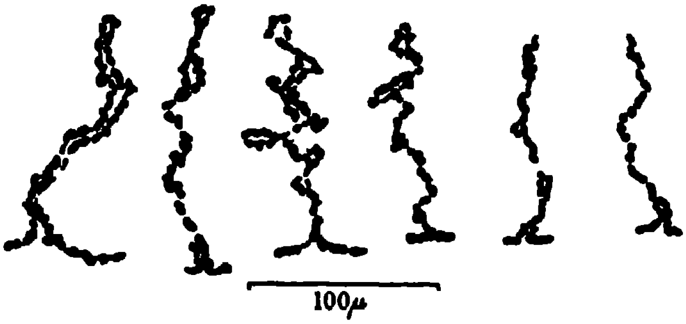


FIGURE 15 Stages in fusion of double capillary plexuses in intertubular septa 48 hr of life

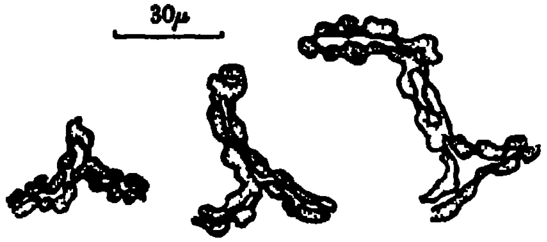


FIGURE 16 Double plexus in early stages of formation of interalveolar septa 48 hr of life

By collapse of capillaries and adherence of endothelium

Such a method of growth has not, so far as I am aware, been described By increasing the numbers of intercapillary spaces as a result of local adherence of their walls it would permit of enlargement of the capillary bed without loss of its complexity Such a method would permit of increase in numbers of capillaries within the existing dimensions of the plexus

Evidence for this view is derived from observations on injected lungs fixed *in situ*

In all injected lungs during the period of growth, minute circular spaces can be found measuring 2 to 3μ in diameter (figure 17) They are found in what would otherwise be very wide capillaries Their edges are clear and well defined and they contain no trace of the injection mass They appear, therefore, to be minute intercapillary spaces They are only very rarely observed in the adult rabbit's lung, as would be expected if the effect is related to growth

The effect is not apparently due to blockage of a capillary by a leucocyte, so that the injection mass is excluded from a small portion of the capillary In preparations stained for nuclei the majority of these spaces are unrelated to a nucleus Moreover, the size even of a leucocyte or endothelial nucleus is much larger than the average size of these spaces, so that the whole cell of the leucocyte must be larger still

More significant evidence comes from the injected partner lung which has been distended to maximum capacity by intratracheal injection It would appear that distension has not had the effect of enlarging these minute spaces and thus of reducing their numbers It appears, indeed, that their frequency is about the same and that they are of the same order of size, namely, 2 to 3μ If therefore such minute spaces are found in the distended lung, what, it may be asked, do they represent in the undistended partner? For this effect there can only be two possible explanations Either that 'maximum distension' is not of uniform distribution in the distended lung or that these minute spaces have been newly formed as a result of distension of the lung, which has enlarged those already present

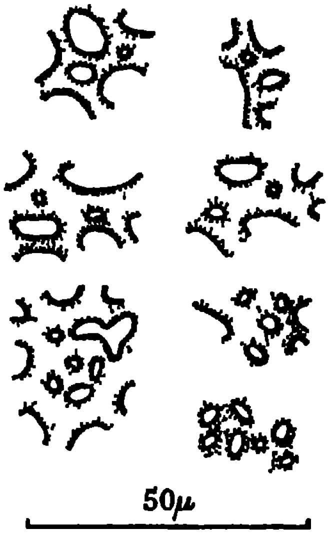


Figure 17 Minute intercapillary spaces in distended partner lungs Term (left) and 24 hr of life (right)

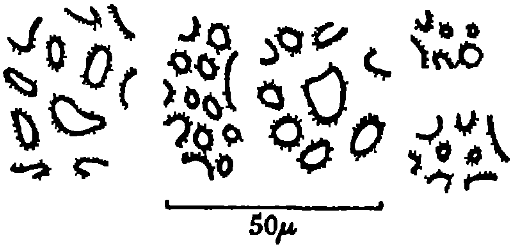


Figure 18 Capillary plexuses in distended lung 48 hr of life

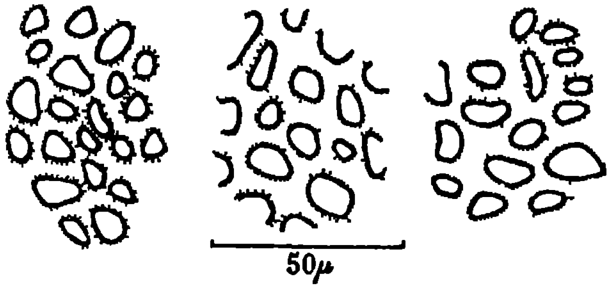


Figure 19 Capillary plexuses in distended lung Adult rabbit

It is probably significant that the range of size of the intercapillary spaces shows greater uniformity in the adult (when enlargement of the capillary bed can be assumed to have ceased) than in the embryo or newborn rabbit (see figures 18, 19) Moreover, figure 20 seems to show that the range of size of intercapillary spaces is rather less in the undistended lung Distension would seem to have enlarged the largest spaces whilst scarcely altering, perhaps even reducing, the size of the smallest The smallest spaces in the distended lung may therefore represent potential spaces in the undistended partner minute areas of adherence between opposite walls of a capillary, unrecognizable by ordinary methods Lastly, between the 23rd day of embryonic life and the 28th day, growth of the capillary plexus is accompanied by a well-marked narrowing of the constituent vessels (figures 21, 22, 23) This is some evidence that growth takes place by multiplication of intercapillary spaces than by multiplication of the capillaries themselves

These observations, though not conclusive, suggest the possibility of an undescribed method of capillary proliferation by multiplication of the intercapillary spaces Large areas of the capillary bed of the lung are kept physiologically closed (Wearn *et al* 1934) The mechanisms of closure and re-expansion are unknown, but, during the period of growth, closure suggests capillary collapse and the possibility of adherence of the endothelial lining Re-expansion may result in the appearance of new intercapillary spaces By increasing the numbers of intercapillary spaces, a larger surface area could be vascularized without the loss of complexity of the vascular bed which would otherwise occur from stretching Further evidence of this method must be sought from direct observation of the living lung during the period of active growth

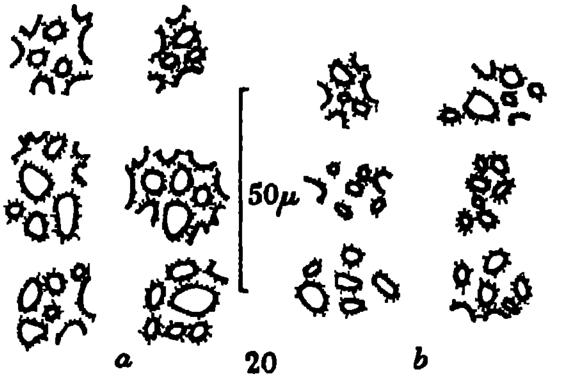
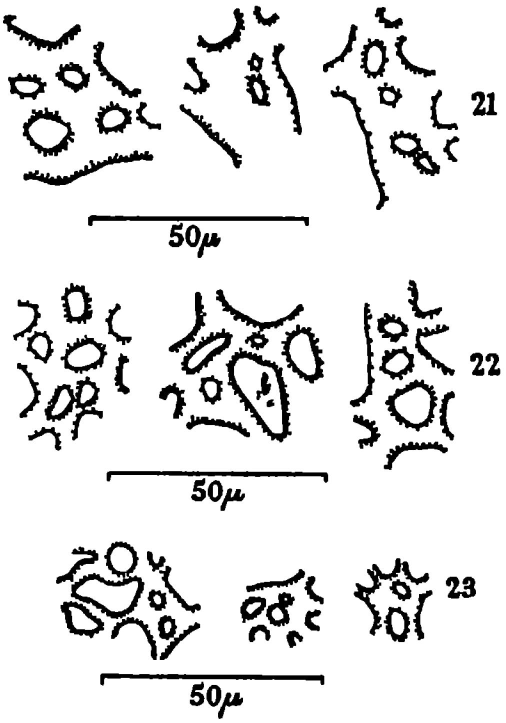


FIGURE 20 Effect of distension of lung upon capillary mesh size from a lung fixed *in situ* (*a*) and from its distended partner (*b*) 24 hr of life



FIGURES 21 to 23 Comparison of capillary diameter at 23 days (figure 21), 26 days (figure 22) and 28 days (figure 23) of embryonic life

HISTOGENESIS OF THE EPITHELIUM OF THE RESPIRATORY TREE (RABBIT EMBRYO)

The description which has already been given of the stages leading to desquamation of epithelium between the 24th and 26th days of the rabbit's embryonic life requires further elaboration The following sections contain further evidence which supports the view that the surface of the alveolus is not covered by epithelium in the normal rabbit after the 26th day of embryonic life

Quantitative data are given first and are followed by analysis of the effects of silver impregnation in the foetus and adult rabbit The interpretation of silver impregnation, undoubtedly, is the heart of the problem of alveolar epithelium which would not have been supposed to exist in the adult lung had silver nitrate not been discovered to impregnate cement lines The results of counts of nuclei in the alveolar septum of the adult rabbit and of dissociation of its structure are next described The results of these four methods of investigation provide strong evidence that the alveolar septum is not covered by any sort of epithelium after the stage of epithelial desquamation in embryonic life is passed

Estimate of volume of epithelium

If drawings of lung fields are made with a camera lucida between the 18th and 24th days, the percentage area* occupied by epithelium increases whilst the height of its constituent cells falls (see table 5) In relation to total lung volume,* the total volume of epithelium is therefore increasing The epithelium succeeds in keeping pace with the ever-increasing internal surface area by stretching laterally with consequent loss of height of its constituent cells Unless cell multiplication occurs, this continual increase in cell volume, together with the lateral stretching of the cells, must ultimately lead to cell rupture Rupture occurs between the 24th and 26th days, and is accompanied by extrusion of nuclei into the respiratory lumen which has already been described

TABLE 5 VOLUME OF EPITHELIUM AND HEIGHT OF EPITHELIAL CELLS

day	% of lung field occupied by epithelium	height of epithelial cells (μ)
18	8	17 5
21	6	—
22	11	7 5
24	14	5 0
26	0	0

TABLE 6 ESTIMATE OF CELL DIVISION IN EPITHELIUM

day	lung volume (ml)	$\sqrt[3]{\text{(lung volume)}}$	ratio increase of $\sqrt[3]{\text{(lung volume)}}$	counted number of cells per 100 μ	calculated number of cells per 100 μ if no growth
	(1) In epithelium of distal tubes which desquamates				
18	0 038	0 336	1	32 ± 1 93	32
22	0 194	0 580	1 72	16 ± 1 73	19
24	0 347 ± 0 07	0 703	2 03	12 ± 2 06	16
	(2) In epithelium of proximal tubes which persists				
18	0 038	0 336	1	32 ± 1 93	32
22	0 194	0 580	1 72	24 ± 1 37	19
24	0 347 ± 0 07	0 703	2 03	26 ± 1 64	16

It is possible to show that cell division is non-existent If a length of wall covered by epithelium is stretched to twice its original length, the number of cells per unit length will be reduced to half the original number From the curve of lung volume, the increase by growth in linear measurements may be calculated ($=\sqrt[3]{\text{(lung volume)}}$) The number of cells actually found per unit length are very close to those expected if the original number of cells per unit length at the 18th day remained the same (see table 6) These results from the distal epithelium, which desquamates, are contrasted with similar measurements from the proximal part of the respiratory tubes, where epithelium persists If the calculation for the 24th day is repeated for the lung volume represented by three times the standard deviation (lung volume = 0·347 ± 0·07), upper and lower values for the calculated number of cells are 20 and 13. Therefore 26 cells per 100 μ is significant.

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* The complete data upon which the mean figures of lung volume and its percentage composition are based will be found in the section on lung growth

The embryological development of the epithelium and its desquamation have already been described. Cell rupture and extrusion of nuclei between the 24th and 26th days are in agreement with the conclusions based upon quantitative data. Taken together they give evidence of degenerative changes in the epithelium which culminate in desquamation at or about the 26th day of embryonic life in the rabbit.

Review of literature concerning epithelial desquamation

The observation that the epithelium of the distal portion of the respiratory tree undergoes degeneration is not new. In the earlier stages of its history, the observation was entangled with the theory of pre- and post-natal flattening of epithelium elaborated by Kuttner (1876) and his followers. The interesting feature is the relatively late appearance of the view that it constitutes evidence for desquamation of an epithelium which is never replaced in the normal adult.

Jalan de la Croix (1883) described nuclear disappearance in the flattened epithelial cells of late pre-natal life and regarded the process as maturation of the 'non-nucleated plate'. In his illustrations of the lung of the foetal pig, Flint (1906) shows clearly the epithelial transformation which occurs at the 22 cm. stage. From being clearly visible cuboidal epithelium, the lining becomes invisible to ordinary methods of investigation and his conclusion is that the cells flatten. Bremer (1904) and Miller (1913, 1932, 1937), whilst admitting the difficulty of seeing it, consider that an epithelium must be present to allow of continued growth of the lung from birth to maturity. Ogawa (1920) described and figured nuclear pycnosis, karyorrhexis and chromatolysis of foetal epithelium and satisfied himself of the existence of non-nucleated plates by the discovery of a single example.

Quantitative evidence of the amount of epithelium which disappears from the lung of the foetal sheep is given by Faure-Fremiet & Dragoiu (1923). The change was associated with increase in the fatty-acid and total nitrogen content of the lung and with a sharp decline in glycogen, which accumulates in the degenerate epithelium in the sheep (and also in the rabbit). The contemporary work of Stewart (1923) on the rat embryo showed that this critical period in epithelial development was associated with fatty change in the cytoplasm of both epithelial cells and of stroma cells in the septal wall. He also described sloughing of the terminal epithelium associated with hydropic (suggesting increased volume of epithelium) and fatty changes in the cytoplasm and with degenerative changes in nuclei of epithelial cells. Though he is very cautious in drawing conclusions as to the lining of the adult alveolus his description of 'flanged epithelium' in the 20-day rat embryo seems to be a more acceptable alternative than to admit 'that capillary endothelium may be in contact with air'. Bremer (1939) also records fatty change in the epithelium and connective tissue of the chick's lung.

Of modern workers, Policard (1926) seems to be the first to strip the alveolus of its disputed epithelium. His argument is based less on interpretations of minute structure than on the derivation of the septal cell from the reticulo-endothelial system. The alveolar septum of the adult is thus of mesenchymal origin since all traces of epithelium have disappeared during embryonic life. Supporting evidence is adduced from Carleton's (1925) results of tissue culture of foetal lungs (to produce epithelial sheets showing fibrinolytic activity, fibroblasts and few active macrophages) and adult lungs (no epithelial sheets but many fibroblasts and numerous, actively phagocytic macrophages)

Following Policard's review, subsequent workers have turned their attention to the capillary bed of the alveolar wall Chiodi (1928) describes its increase during the 5th to 6th month in the cow foetus, when the epithelium desquamates Palmer (1936) regarded epithelial desquamation in the human embryo as the result of capillary proliferation In this interpretation he was followed by Clements (1937), Barnard & Day (1937) and the more recent work of Norris, Kochendorfer & Tyson (1941) and of Ham & Baldwin (1941) These authors, however, do not describe the development of the capillary bed whose double character, produced by two plexuses laid back to back, is described in the older work of Schultze (1871) Their evidence from the human embryo rests upon the appearance of capillaries projecting into the alveolar lumen or penetrating between adjacent degenerate epithelial cells This may partly be due to increased prominence following desquamation of epithelium but, in the rabbit, does not appear to be due to active capillary proliferation by the usual method of buds or loops

Results of silver impregnation

No single factor has exercised a greater influence upon the history of alveolar epithelium than has von Recklinghausen's (1860) announcement of impregnation of epithelial cement lines by silver nitrate The silver is deposited at the cell periphery where it may be blackened by sunlight or by a photographic developer (the latter used by Jeker 1933, by Ritter, quoted Cowdry, 1943, Bensley & Bensley 1935) The deposit is soluble in sodium thiosulphate and in potassium ferricyanide, which serve as useful differentiators in dilute solutions

In perfectly successful preparations no more than these black lines are visible Very commonly, however, a granular deposit is found at or round the nucleus which serves as a useful landmark Unless precautions are taken to avoid folding of the membrane, a granular deposit is likely to occur in the folds and thus to mask, though not to obliterate, an otherwise clear picture In transverse sections of such impregnations, the silver is seen to have been largely deposited at the luminal surface of the cement line (cp Robinow 1936, 1938), though a granular deposit may be observed to extend towards its deeper extremity In such cases, a weak differentiating solution may remove the granular precipitate whilst it leaves the cement line untouched It was probably by such means that Gustav Mann obtained his very perfect results (figures, 24, 25, plate 1)

In less successful impregnations, the cement outlines may show a tendency to be granular, and a fine granular deposit may occupy the cytoplasm of the cell Such areas may exist with others in the same section where impregnation is perfect In the study of a capillary bed, for example, such imperfect areas have the advantage of outlining the capillary bed in one portion and its constituent endothelial outlines in another It may, indeed, be impossible to reconstruct the extent of a capillary bed from a successful impregnation of its endothelial outlines alone

Impregnation in the foetal rabbit

At the 23rd day of development when ordinary histological examination shows a continuous nucleated epithelium, intratracheal injection of silver nitrate reveals the cell outlines as a regular meshwork (figure 26) In the alveolar ducts the cell outlines are distinctly larger than is the case in the bronchioles or in the extreme tips of the tubes This is probably the result of distension by the injected solution In all outlines nuclei are clearly visible either as a finely granular deposit of silver or stained by haematoxylin or neutral red

At the 25th to 26th days, the silvered outlines present the classical picture of small, nucleated cells and large non-nucleated plates (figure 27) The changes are not distributed uniformly in the lung Some lobules show the appearance whilst others do not The most advanced portions show a wide-meshed network of lines among which lie smaller areas Both types of outline contain nuclei, the larger areas being sometimes bi-nucleate though the smaller never have more than one Occasionally the larger areas are non-nucleate The nuclei of the larger areas are themselves larger than are those of the small cell, and they do not stain so intensely with a nuclear counterstain The larger nuclei are certainly to be identified with the swollen, degenerate nuclei of the unsilvered haematoxylin preparation where the same cell is of smaller size The larger size of these cell areas is probably therefore an effect of distension by injection of silver nitrate The termination of bronchiolar epithelium is now clearly marked, and its close-meshed, nucleated network undergoes a sudden change into that just described

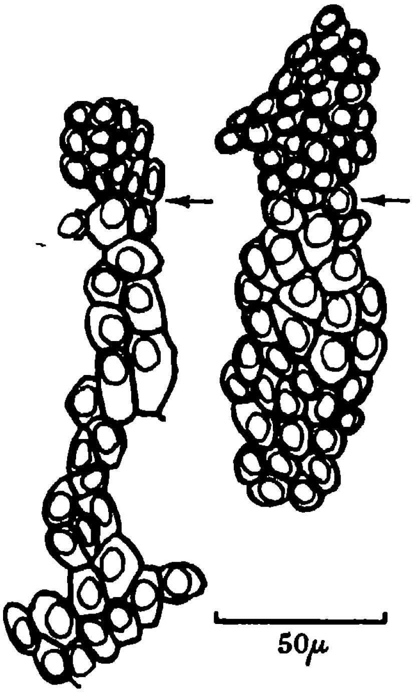

FIGURE 26 Silver impregnation of lung at 23rd day Termination of bronchiolar epithelium is marked by an arrow in this and subsequent figures

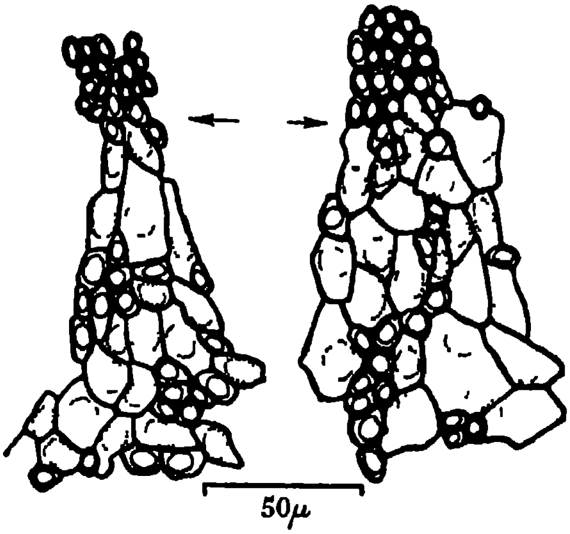

FIGURE 27 Silver impregnation of lung at 25th day This is the classical picture of small nucleated cells and 'non-nucleated plates' Of the latter, however, most are nucleated

By the 27th day, the contrast between large and small cell outlines is maximal (figure 28) Without a knowledge of the previous stages it would not be suspected that the largest areas were the result of distension of degenerate cells in the original epithelium Degenerate nuclei may or may not be found Still more significantly, the pattern of the mesh shows early signs of irregularity Lines may be found which no longer link up with their neighbours and thus give rise to larger areas of very irregular outlines Nevertheless, a tolerably regular mesh is still present over large areas, and it is probable that these minor degrees of irregularity would have been overlooked if attention had not been specially directed to finding them Owing to the thickness of the septa, no difficulty is found in recognizing beyond any doubt that these meshworks are true surface meshworks Such a picture in the distal portion of the lung renders the termination of bronchiolar epithelium even more distinct than was found at the 25th to 26th day

28th to 31st day The surface impregnations have now become so exceedingly irregular that considerable difficulty is found in drawing them (figure 29) The lines are now fragmentary, incomplete and irregular, and thus contrast with the small regular mesh of bronchiolar epithelium The only trace of former regularity is found in alveolar septa exposing one surface to a lumen in which a few lines connecting the relatively numerous small nucleated cells give rise to patterns of tolerable regularity It is in these situations that small, regular portions of the mesh persist after birth and may even be dimly recognized in the adult This description is in harmony with Jeker's (1933) findings in the kitten, with the qualification that what the kitten accomplishes by the second or third week of life, the rabbit has accomplished by term

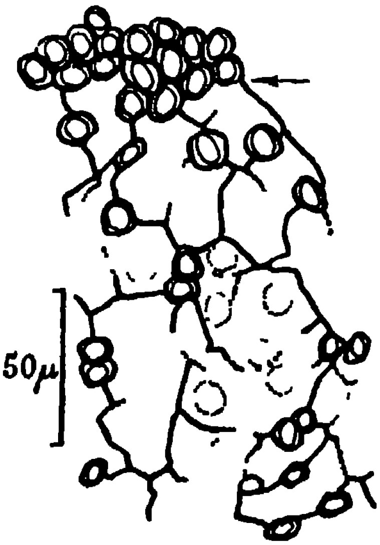

FIGURE 28 Silver impregnation of lung at 27th day Early irregularity of the impregnated meshwork is seen Several cells have lost their nuclei

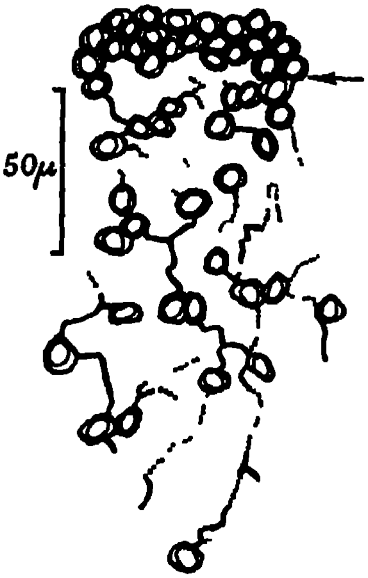

FIGURE 29 Silver impregnation at 31st day The impregnated outlines have become exceedingly irregular Nuclei have disappeared

A point worthy of emphasis is the size of the small nucleated cell It appears to be distinctly smaller at term than were the corresponding structures at the 25th day Since the small nucleated cell of silver impregnations has been regarded as identical with the alveolar phagocyte, the slight difference in size raises the question whether the small nucleated cell (apparently of epithelial origin) of the 25th day persists to become the alveolar phagocyte The smaller size of the corresponding cell at term suggests an alternative possibility that certain more deeply situated histiocytes may reach the surface during the process of epithelial desquamation and may there round themselves off No clear evidence of the origin of the alveolar phagocyte is given by this material

Impregnation in the adult rabbit

As thus described there is no difficulty in tracing the stages of development between the pattern of the foetal mesh and that of the adult At almost all periods the impregnation can be related to the more ordinary histological picture of haematoxylin and eosin An exception is found in the impregnation of subpleural alveoli or those septa which expose but one surface to a lumen

Following intratracheal injection of silver nitrate into the lung of the adult rabbit, absolutely no surface impregnation can be recognized over most of the lung surface At the most a granular deposit is found which defines folds and irregularities in the film-like septa Where this has occurred evenly it may be possible to define intercapillary spaces as pale areas outlined by a granular border bearing a superficial resemblance to true impregnation of epithelium

It is, however, possible to recognize traces of true epithelial impregnation in subpleural alveoli (figure 30, plate 1) or in those which abut against an interstitial structure (figures 31, 32, plate 1) In these situations, the picture of small nucleated cells and large non-nucleated plates may be so clear as to recall the 26th day stage in the foetus In silvered preparations the size of the large areas is between 600 and 800 sq μ or more The smaller areas clearly nucleated, are rather larger than an average intercapillary space The lines joining them are not limited to the area of the capillary bed, since they do occasionally cross an intercapillary space and they appear to be limited to the surface

Such observations have stimulated fruitless search in the rest of the lung, and by multiplying modifications of technique have sought to obtain unequivocal results in the largest part of the lung surface No such evidence has been obtained from the rabbit Much of the criticism of the silver method is based upon its inconstant or capricious results, and the locally successful results in the rabbit were for long attributed to such behaviour Impregnations of foetal lung clear, fresh and entirely convincing were a constant challenge to further search in the adult Such a situation is not easily resolved Recognition of stages leading to irregularity of impregnation in the embryo showed that further search in the adult rabbit was equivalent to looking for something which did not exist It has already been suggested that the inequality of size between the large and small impregnated areas of the foetus is the result of stretching of degenerate cell envelopes by injection of silver nitrate solution Similar reasoning will account for the preservation of traces of the original epithelium in the subpleural alveoli of the adult rabbit By far the largest part of the surface area of the lung is subjected by growth to considerable deformation as the result of deformation by septa (to be described in detail later) Epithelial remnants may therefore be expected to be distorted beyond recognition, and none, indeed, can be recognized over the largest part of the surface The mean size, however, of subpleural alveoli, or of those abutting against an interstitial structure, is considerably larger (as noted by Schultze 1871, Ogawa 1920) In the central parts of the lung 25 to 28 septa can be counted over 1 mm length—in subpleural alveoli only 15 to 18 are found This suggests that their manner of growth is different Whereas 'normal' alveoli distend and subdivide at the same time by evocation of septa, subpleural alveoli are probably distended by growth to a greater degree with less accompanying subdivision There may therefore be less distortion of their luminal surface

Review of the literature concerning silver impregnation

The earliest signs of controversy concerning the lining of the pulmonary alveolus appear in 1843, when Thomas Addison wrote that he was 'fully persuaded that pathologically they (manifestly elastic air cells) present none of the attributes of a mucous membrane as Reisseisen and others would lead us to believe' The choice evidently lay between a continuous nucleated epithelium or bare capillaries Rainey (1855) adopts the latter alternative and declares that proof depends upon seeing the epithelium *in situ* and detached and following one into the other Publication by von Recklinghausen (1860, 1862) of a method for impregnating cell outlines by salts of silver had the effect of adding a third interpretation of structure of the alveolar wall Passing through the hands of Kolliker (1854, 1881) it became the commonly accepted teaching At the same time the unsuccessful use of the method (perhaps partly dependent on species differences) gave encouragement to the two existing schools of thought whose subsequent development is most easily considered after toe new interpretation has been analyzed

In the field of comparative anatomy, Elenz (1864) and Eberth (1864) obtained results of such importance that Kolliker, who had previously (1854) described a continuous nucleated epithelium, changed his opinion (1881) He accepted the doctrine of small nucleated cells lying singly or in small groups between the larger non-nucleated plates which together formed a complete lining to the alveolus As a rule the amphibian lung showed an epithelium formed by large nucleated squames whose nuclei lay in the intercapillary spaces Other species showed an intermixture of small cells with the squames In certain reptiles, the small nucleated cells were numerous and sometimes appeared to have become separated from what was interpreted as the non-nucleated, film-like extension A similar condition was described in man In birds, no epithelial investment was demonstrable in the distal (respiratory) portions of the lung Elenz, Oppel (1905) and Schultze (1871) considered nevertheless that an epithelium was present, and Eberth thought he recognized an occasional flat cell Ogawa (1920) considered that an alveolar epithelium does not exist in birds He modified certain conclusions of Elenz, but in general confirmed the conclusions of Kolliker In addition, therefore, to producing very convincing preparations, Elenz and Eberth derived strength from the discovery of a series of stages whereby the epithelium of the mammalian lung could be derived through reptiles to an amphibian ancestor by modification of the lining cells of its terminal (respiratory) portion This evidence, together with the fundamental desire to preserve in the lung 'the regulator effect usually exerted by epithelium on subjacent tissue',* 'satisfied tidy minds'† (an important action), convinced Kolliker and is to-day accepted as current teaching

Doubts, however, persisted, in spite of ingenious modifications by the Bensleys (1935) of the silver technique Three modern workers using silver have reached the conclusion that the alveolar wall is bare (Josselyn 1935, Loosli 1935, 1937, Clements 1937) Their conclusions are in part derived from a scarcely veiled mistrust of silver impregnation To anyone who has seen the preparations (see figures 24, 25, plate 1) made by Gustav Mann in the Histological Department of Oxford University, it is clear that the appearance must be due to impregnation of some sort of cell outline The possibility of artifact, or impregnation of folds, fibres or red blood cells is not seriously to be considered Policard's (1938) off-hand dismissal* of their identity with any sort of cell boundary seems to me to be unsubstantiated by examination of such preparations

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* The phrase comes from my friend Dr N M Hancox of the Department of Physiology, Liverpool University

† Professor G R Cameron, F R S, *Lancet*, 11 January 1947

However, in many of the illustrations of the older workers, a peculiar irregularity of the surface meshworks is seen Kolliker's figure shows it (1881, figure 10) and similar irregularity is found in the drawings of Sobotta (1903) and Merkel (1902) Often attributed to technical error or to the capricious results of silver (Miller 1937, Carleton 1938, Policard 1938), Jeker (1933) was able to trace the development of such irregularity in the cat embryo For a satisfactory discussion to be possible this effect must be taken into account Bargmann (1936), whilst supporting alveolar epithelium, relates this irregularity both to the classical theory of Kolliker and to the diametrically opposed theory of naked capillaries of Seemann (1931) by supposing that the non-nucleated plates survive to the adult in a modified form If non-nucleated plates may lose their outlines to persist in a modified form, how much more need they lose to suffer total annihilation?

The hypothesis that the alveolar wall is lined by a continuous nucleated epithelium received support from Chrzonszczewsky (1863) using the silver technique Modern adherents of this view have come to rely less and less on silver impregnation, and the main weight of the argument has ceased to be derived from normal lungs Miller (1937) thus relies upon pneumonia, Cowdry (1925) upon Jagziekte, a disease of sheep, and Young (1928) upon experimental collapse of the lung In relation to the silver nitrate method, the difficulty of this school is to explain away the appearance of non-nucleated plates Having done so (Miller, 1937, pp 59, 66) they are faced with a far more serious difficulty The number of nuclei in the normal alveolar septum is not sufficient to provide the highly cellular epithelium which Miller illustrates (1937) Josselyn (1935) had already called attention to the fact that nuclei, other than those of endothelial cells, 'are so few in number in most cases that they appear quite incidental' This aspect is considered in detail in the next section

Nuclear counts of the alveolar septum of the adult rabbit

In thick sections of the lung where it is possible to study the whole extent of an alveolar septum, it is a striking fact that the distribution of nuclei is not regular In material of which the capillary bed has been injected by weakly coloured carmine-gelatin, and subsequently counterstained by haematoxylin, surprisingly large areas are devoid of any nuclei whatever (see figure 33)

Assuming that the capillary bed of the alveolus is invested by endothelial cells, it should be possible to discover the size of these cells by counting endothelial nuclei in measured areas of the septum in which the capillary bed has been defined It should also be possible to discover whether the total number of nuclei is sufficient to provide a complete investment for the capillary bed and also to provide epithelium for both surfaces of the alveolar septum By excluding leucocytes and by identifying nuclei of endothelial cells and alveolar phagocytes, the remaining nuclei could be regarded as belonging to epithelium No such nuclei were found

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* 'Mais on peut affirmer qu'ils n'ont rien de commun avec des limites cellulaires', loc cit (p 61)

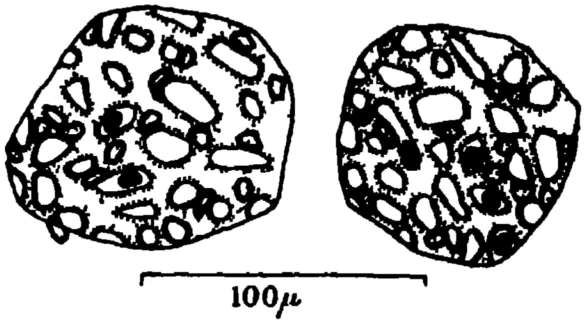

FIGURE 33 Nuclei of endothelial cells (black outline) and of alveolar phagocytes (solid black) in alveolar septa viewed in plan, in which the capillary bed has been injected and is represented by stippling Adult rabbit

TABLE 7 EXTENT OF CAPILLARY BED IN ALVEOLAR SEPTA ADULT RABBIT

example	area of septum (sq μ = S)	area of capillary bed (sq μ = C)	$\frac{C \times 100}{S}$ (%)	surface of capillary bed (sq μ = π × C)
1	8,260	6,500	79	20,400
2	7,280	6,220	85	19,600
3	6,530	5,080	78	15,900
4	6,650	5,180	78	16,300
5	7,100	5,680	80	17,800
6	5,770	4,320	75	13,600
7	7,740	5,900	76	18,500
8	5,770	3,930	68	12,300
9	4,000	2,700	67	8,480
10	4,180	2,780	67	8,750
11	2,830	1,790	63	5,630
12	2,780	1,960	70	6,150
13	3,450	2,220	64	7,000
14	2,390	1,920	80	6,030
15	3,600	2,710	75	8,500
mean	5,220	3,920	75	12,300

TABLE 8 NUMBERS OF NUCLEI IN ALVEOLAR SEPTA ADULT RABBIT

	numbers of nuclei			
example	endothelial	alveolar phagocytes	total	size of endothelial cell (sq μ)
1	33	4	37	620
2	34	6	40	580
3	25	5	30	640
4	16	2	18	1010
5	16	1	17	1110
6	13	4	17	1040
7	16	4	20	1160
8	14	6	20	880
9	13	5	18	650
10	10	5	15	875
11	9	5	14	630
12	11	3	14	560
13	7	4	11	1000
14	10	4	14	600
15	13	2	15	660
mean	16	4	20	800

Tables 7 and 8 summarize the observations on fifteen septa in a rabbit's lung The capillary bed occupies about 75 % of the total area of the septum By multiplying the area of the capillary bed by π, an approximation can be obtained to the total surface area of the capillary bed Dividing this estimate by the total number of endothelial nuclei, the average size of an endothelial cell is of the order of 800 sq μ Four cells, identified as alveolar phagocytes, remain, and if it is assumed that they are capable of forming a complete epithelial investment to both surfaces of the septum, their size would need to be 2600 sq μ If allowance is made for folding of the cells round the capillary bed the average size would be almost 4000 sq μ Even if we assume that nuclear identification is incorrect and that all types of cell may be called upon indiscriminately to cover the capillary bed and both surfaces of the septum, the average size of these twenty cells would need to be 1360 sq μ We may conclude confidently that a continuous nucleated epithelium does not exist in the normal adult rabbit

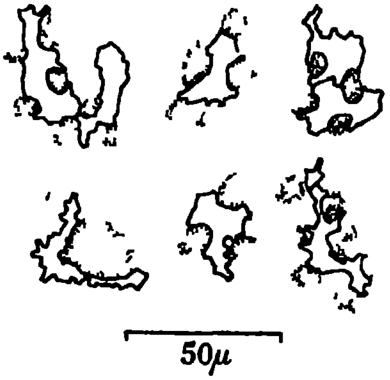

FIGURE 34 Impregnated outlines of endothelial cells from the capillary bed of alveolar septa Intercapillary spaces are stippled Adult rabbit

This estimate of endothelial cell size is seen to be much larger than that of the isolated cells shown in figure 34 This is due to two causes a greater degree of distension was deliberately obtained in the lungs from which counts of nuclei were made in order to facilitate their study, and allowance has been made for curvature of the wall of the capillary Both these factors will therefore reduce the calculated size of the endothelial cell The volume of lungs used for nuclear counts is about 1 5 times the volume of the silvered lungs, making measurements of area too high by 1 3 An approximation to the second factor is given by $\frac{1}{2}\pi$ or 1 77, since not more than two endothelial cells enclose the capillary wall, though one cell may sometimes do so The total amount therefore by which area measurements in tables 7 and 8 are too high is 2 4, and division by this factor gives the mean cell area of flattened capillary endothelial cells as 310 sq μ This figure is in harmony with measurements of area of capillary endothelial cells which I have made in the skin of the adult rabbit

Results of dissociation of the alveolar septum

Several attempts were made to dissociate the structures composing the alveolar wall of the rabbit's lung by perfusion through the pulmonary artery at pressures of 50 mm Hg Using normal saline as perfusate, heavy oedema occurred within 15 min , but histological examination showed no more than widely dilated capillaries Using formol-Muller solution, histological examination showed that three grades of dissociation had been produced in three rabbits A similar effect following perfusion of fixative seems to have been noticed by Schultze (1871) The first rabbit showed heavy oedema with slight evidence of rupture of the alveolar septa In the second considerable rupture with oedema was present In the third, a generalized interstitial dissociation with no rupture and a minimal oedema within the alveoli had been produced, a condition which could be described as interstitial oedema

Histological examination of this lung showed that the effect had been to dissociate the capillaries with the protoplasmic films separating them from the lumen of the alveolus and thus to separate the constituent structures of the alveolar wall by accumulation of fluid within its substance The most striking feature was the thickness of the septum The typical appearance of congested capillaries of the normal alveolar wall, bulging into the lumen to either side of the delicate septum, had completely disappeared Instead, the dilated capillaries were situated between parallel lining membranes of extreme delicacy The continuity of the lining membrane was occasionally interrupted by a septal cell, but over long tracts no nuclei were to be seen on the luminal surface (figures 35, 36, 37, plate 1) Endothelial nuclei, recognizable by their minute speckling with Heidenhain's iron haematoxylin, lay more often in the substance of the alveolar septum than in contact with the surface Nowhere was there an orderly nor numerous arrangement of nuclei to suggest the presence of a nucleated epithelium In many alveoli not one nucleus was to be seen in contact with the lumen

Where they were in closest apposition to the alveolar lumen, the capillaries appeared to be separated from it only by an almost structureless membrane containing reticulum fibrils Not once was this membrane found to be lifted off or separated from the endothelial cytoplasm, and normally both appeared to be in direct continuity It was not possible to be certain whether this lining membrane was merely the stretched cytoplasm of endothelial cells, but appearances frequently suggested that this was the case If such is the case, the lining membrane is that part of the endothelial cell excluded from contact with the vascular lumen The distribution of mitochondria in the cytoplasm of endothelial cells was thought to show that similar bodies in that portion of the lining membrane nearest to the capillary were also mitochondria

Close attention was paid to the points at which bronchiolar epithelium came to an end to be replaced abruptly by the lace-like structure of the alveolar septum (figure 38, plate 1) A capillary was often in direct contact with the lateral wall of the last epithelial cell Elsewhere a basement membrane of reticulum intervened between the capillary plexus and the epithelial cells

It appeared, therefore, that the capillary bed was everywhere ensheathed by a delicate membrane containing reticulum fibrils The impression was formed that the membrane was continuous with the cytoplasm of endothelial cells No evidence was obtained of the existence of a continuous nucleated or non-nucleated epithelium which could be detached from the capillary

PART 2 LUNG GROWTH

INTRODUCTION

The histological picture of lung development is everywhere consistent with the view that alveolar epithelium ceases to exist after a certain stage in the embryonic life of the rabbit It is, however, easily recognized that the complexity of the lumen of the foetal lung increases as the result of branching and rebranching It might be supposed that the invasive activity of epithelium was displayed to great advantage After the 26th day further subdivision occurs and the complexity of the lumen increases still further However, at the 24th day, a continuous epithelium has ceased to exist Yet the lumen has continued to grow and to become more subdivided

The growth of the lumen can only be investigated when quantitative data for total lung volume are known When lung volume is known, the percentage distribution of lumen in stained-sections of the lung can be applied to total lung volume Volume data are therefore the point of departure in this second part of the investigation of lung development

These results can next be compared with quantitative estimates of 'complexity' of subdivision of the lumen A simple method, capable of interesting mathematical development, has been used to measure internal surface area of the lung Moreover, it has been found possible to distinguish increase in surface area resulting from simple distension from that which must occur as a result of increasing complexity of branching It is found that internal surface area increases as a result of increased subdivision long after desquamation of epithelium has occurred

METHODS

The numbers of animals are shown in table 9

TABLE 9 SERIES OF EMBRYO AND POST-NATAL RABBITS

day	numbers of animals	observations of lung weight	observations of lung volume
18	2 (mean)	2	—
20	4 (mean)	4	—
23	2 (mean)	2	—
24	3 (individual)	3	—
26	7 (mean)	7	—
	5 (mean)	5	—
	11 (individual)	11	—
29	2 (individual)	2	—
30	15 (individual)	15	15
31	3 (individual)	3	—
	3 (individual)	3	3
	3 (individual)	3	3
	4 (individual)	—	4
(birth)			
3 hr	5 (individual)	—	5
4 hr	1 (individual)	—	1
6 hr	5 (individual)	—	5
1 day	4 (individual)	—	4
	10 (individual)	—	10
2 days	2 (individual)	—	2
4 days	2 (individual)	—	2
5 days	3 (individual)	—	3
10 days	3 (individual)	—	3
3 months	3 (individual)	—	3
adult	4 (individual)	—	4

The mother was anaesthetized intravenously with 1 0 ml nembutal per kg body weight, the abdomen was opened and the uterus rapidly incised The foetuses in turn were removed from the uterus and strangled without opening the amniotic sac Care was taken to avoid the occurrence of premature respiratory movements caused by rough handling After death, the trachea was tied with cotton The body weight of the foetus was then determined after removal of the placenta and membranes

In the larger lungs at term and in those which had breathed, lung volume was measured directly (as described below) in lungs which had been fixed for 48 hr within the unopened thorax In the smaller, normally fluid-filled lungs of the embryo, direct measurement of volume was found to be impracticable and volume was calculated from lung weight and lung density

SHRINKAGE OF THE LUNG PRODUCED BY FIXATION

Fixation of the embryo lung in 10 % formol saline affords so much protection against trauma to the jelly-like consistence of the lung when fresh, that all manipulation in these experiments has been delayed until fixation was complete This procedure has the disadvantage that measurements of weight must be made on fixed lungs It becomes necessary to establish whether the effect of fixation upon lung weight can be regarded as a constant and if not, to prepare a calibration curve between fresh and fixed lung weight

In the following preliminary experiments the fresh thoracic contents were removed as carefully as possible Their fresh weight was determined and the whole was then fixed in formol saline Weight was determined at 1, 3, 24, 48 hr and 3 days after fixation To remove the thoracic contents is not a difficult matter, and can be performed in the confidence of having avoided trauma to the jelly-like lungs and of preserving their fluid contents To separate the individual fresh lungs is very much more difficult though very easy after they have been fixed

When fixed in formol saline shrinkage of the lungs is found to be variable, and the weight of the fresh embryo lung is reduced by an amount which depends upon three factors

(1) The time after immersion in fixative An initial fall, maximal between 1 and 3 hr after immersion, is succeeded by a slow rise to a figure somewhat less than the weight of the fresh lung Measurements of weight have been made in all cases at 48 hr after immersion of the embryo lung in formol saline

(2) The age of the embryo At the 24th day of the rabbit's 32-day gestation period, the effect of 48 hr fixation in formol saline is to reduce the weight of the fresh lung by 1 % At the 26th day about 5 % is lost, and at the 28th and 30th day about 10 and 15 % respectively The effect is probably due to loss of water following shrinkage of the lung, and the size of the effect is due partly to the degree to which the lung contains a lumen Earlier than the 24th day when about 25 % of total lung volume is occupied by lumen, shrinkage is slightly below 1 % Moreover, in the completely collapsed lung of the adult rabbit loss of weight by fixation amounts also to no more than 1 % It is therefore justifiable to regard shrinkage of pulmonary interstitial tissue as a constant of negligible importance

(3) Respiration *in utero* If half the embryos in a litter older than the 26th day are strangled before respiration has occurred, lung weight of these foetuses is reduced by the amounts shown in the preceding paragraph Intra-uterine respiration is then encouraged

in the remaining foetuses by tapping the unopened uterus Loss of weight is found to be considerably greater in most of the members of this group It is no doubt due to the increased stretch (and thus to increased capacity to shrink) resulting from inhalation of liquor amnii A similar effect was noted in the control experiment of the collapsed lung fixed in formol saline The control lung was placed in normal saline and gained 6 % of its original, fresh weight in 4 hr It was then placed in formol saline for 48 hr, by which time it had lost 1 % of its original fresh weight—the same loss as was found in the collapsed lung which had been fixed at once If, however, loss of weight is calculated as loss of greatest weight (as must be the case in embryos which have inhaled liquor amnii), loss of weight in the control collapsed lung is 7 0 %

Premature respiration will therefore increase the amount by which the embryo lung shrinks during fixation Though it is possible to discard those foetuses which show intra-uterine respiration during the experiment, it is not possible to affirm that no respiration has occurred in the remaining foetuses before the experiment was started Therefore the factor by which fresh lung weight differs from fixed lung weight has been calculated from the mean loss of weight of lungs from both groups and not merely from that group in which respiration *in utero* was not observed

TABLE 10 SHRINKAGE OF THORACIC CONTENTS DURING 48 HR FIXATION

	percentage of original weight lost		
day	no respiration	mean of both groups	premature respiration
24	0 2	1 5	
	1 0		
	3 3		
26	3 4	8 5	12 8
	4 5		14 0
	5 0		14 6
	5 9		
	7 8		
28	9 8	14 2	16 7
	9 8		17 6
	11 6		20 3
	13 5		
	13 8		
30	12 0	15 5	17 5
	14 2		20 2
	14 2		
	14 9		

TABLE 11 CORRECTION FOR SHRINKAGE DURING FIXATION RABBIT

day	correction for weight	correction for volume*	correction for length†
24	1 015	1 014	1 005
26	1 09	1 040	1 013
27	1 14	1 08	1 025
28	1 16	1 10	1 033
29	1 175	1 12	1 037
30	1 182	1 125	1 04
31	1 19	1 135	1 043

* Obtained by dividing the correction for weight by lung density = 1 05

† The cube root of corrections for volume

Shrinkage of air-filled lungs

The volumes of air-filled lungs have in all cases been measured after intravenous perfusion of fixative whilst the lung was contained within the unopened thorax Attempts have been made to discover whether or not such air-filled lungs fixed *in situ* are shrunk by fixation

Table 12 shows that no significant shrinkage is found between the volume of a wax cast of the thoracic cavity and the volume of the fixed thoracic contents in pairs of animals of the same body weight These measurements were made upon 10-day-old and adult rabbits

TABLE 12 SHRINKAGE OF AIR-FILLED LUNGS

age	body weight (g)	volume of cast (ml)	volume of thoracic contents (ml)
10 days	138	9 8	10 3
	140	15 0	12 7
		mean 12 4	11 5
adult	1840	65 0	71 5
	1840	79 0	85 5
		mean 72 0	78 5

Treatment of results

The fitting of curves to growth data has been the subject of many discussions, and no agreement has been reached as to the most suitable type of curve In view of this situation and of the purpose of the present investigation it has seemed unnecessary to attempt to fit a curve Since successive groups of observations were made at relatively short intervals it has been deemed adequate to intrapolate linearly between adjacent means in order to obtain, when required, an estimated mean value at intermediate times

Fixed lung weight Embryos fixed in 10 % formol saline after tying the trachea and after opening the thorax in order to obtain rapid penetration of fixative After 48 hr the lungs and heart were carefully removed from the thorax and the lungs were separated after tying the hila Excess fluid was gently removed from the surface with cotton-wool, and fixed lung weight was determined in a weighed watch-glass

Lung volume Determinations of lung volume at the 30th day were carried out as described below after weighing fifteen lungs which had been fixed for 48 hr

In all other cases a different procedure was adopted since the lungs had breathed The newborn or older rabbit was given 0 5 ml nembutal by intraperitoneal injection When respiration had ceased, the abdomen was opened and 2 ml of 10 % formol saline was slowly injected into the inferior vena cava The whole foetus was then immersed in formol saline After 48 hr the trachea was tied and the lungs and heart carefully removed from the thorax After tying the hila, the lungs were gently separated and their volumes determined by displacement of water Smaller lungs were placed in a burette reading to 0 1 ml The larger lungs were placed in a burette of larger calibre, and after re-levelling the volume of displaced fluid was collected in the smaller burette reading to 0 1 ml, which was placed below By 'lung volume', therefore, is meant volume of the lung fixed *in situ*

Percentage of lumen and interstices From histological material, whose preparation has been described in part 1, ten fields, including as far as possible only the terminal lobules, from each lung were drawn with a camera lucida using a sixth-inch objective Two sets were prepared In the first, only lumina were drawn, in the second, only the basement membranes The spaces were then cut out and weighed together The remaining parts were weighed, added to the spaces and both expressed as a percentage of the total The assumption was made that the composition of an average volume of the lung was the same as that of the average of the ten fields The figures were then applied to lung volume to obtain the data in tables 21 and 23, which therefore represent the composition of a lung lobule of the same size as the lung or the composition of an imaginary lung from which all the larger structures (arteries and bronchi) have been removed

Counts of septa Using a sixth-inch objective, five fields from each lung were drawn on squared paper and the intersections of the lumen with eighteen lines were counted Two sets of drawings were prepared, counting intersections with the lumina in one and with the basement membranes in the other Each line measured 308μ The total grid length was therefore 5550μ or 0 555 cm So far as possible, fields were chosen where the larger structures (arteries and bronchi) were absent

For a better understanding of the implications of this method, I am indebted to Mr C A Rogers of the Department of Mathematics, University College, London I quote, with his permission, from a letter in which he draws attention to a formula by which the surface area of a branched lumen can be related to its complexity of branching He says

'Suppose that the total volume of a lung or of a lobe of a lung is V and that the surface area of the lumen is S Suppose that a histological section is taken at random from this lung or lobe and that it is drawn upon a system of lines (squared paper) of total length l Suppose further that the lines of total length l cut the surface of the lumen n times It can be proved (the proof is appended) that the average value of n obtained by repeating this process a number of times will be given by the formula

$$n = \frac{lS}{2V} \tag{1}$$

So if l is the length of lines of the two systems of the grid reduced to the appropriate scale for the magnification factor of the microscope and n is the average of the number of intersections obtained from the study of a section, then an estimate of the ratio of the internal surface area S to the volume V of the lung or lobe is given by

$$\frac{S}{V} = \frac{2n}{l} \tag{2}$$

There are two quantities of biological significance which may be calculated The first is the surface area S given by

$$S = \frac{2nV}{l} \tag{3}$$

The second quantity of significance is the non-dimensional ratio

$$\frac{S}{V^{\frac{2}{3}}} = \frac{2nV^{\frac{1}{3}}}{l} \tag{4}$$

This is a well-known criterion of the complexity of the convolutions of a surface of area S packed into a volume V

Proof of formula (1) *by C A Rogers*

Consider a volume V of lung Let S be the surface area of the lumen contained in the volume V Let G be a grid of lines of total length l, the size of the grid being small in comparison to V (see figure 39) We show that if G is moved by a simple translation to a random position in the volume V

(each position being equally likely) then, on the average, the number of intersections of the lines of G with the surface S will be

$$n = \frac{lS}{2V}$$

We first consider the case when all lines of G are parallel to some fixed direction For convenience we choose an origin O and rectangular Cartesian co-ordinate axes OX, OY, OZ, with OX in the direction of the lines of G Consider an element of length δl of one of the lines of G Let P_0 be the end-point of this element with the lesser x co-ordinate We suppose that the element is moved by a translation to a random position in V and show that, provided δl is sufficiently small, the chance that the element has an intersection with S is

$$\frac{S\delta l}{2V}$$

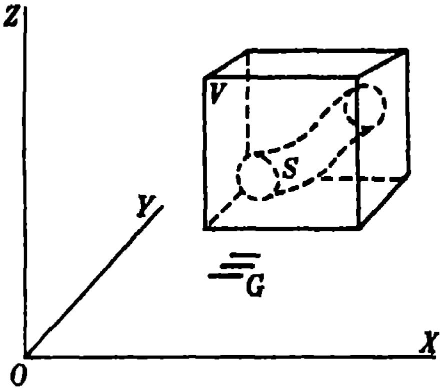

FIGURE 39 In this diagram, V has been taken to be a cube, S to be a cylinder and G to be a system of three equal lines

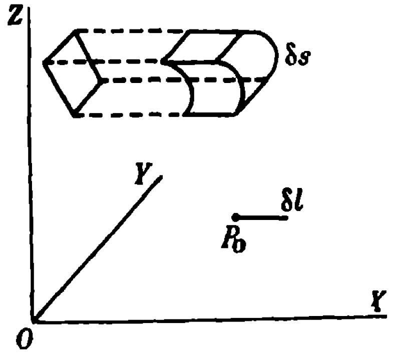

FIGURE 40

Consider an element with area δs of the surface S We suppose that the element is so small that it may be regarded as flat, and we suppose that θ is the acute angle between the normal to the element and the OX axis Now when the element δl of G is moved into V it intersects the element δs of S if, and only if, the point P_0 is moved into the skew prism generated by moving the element δs by a translation in the direction from X to O through a distance δl (see figure 40)

The volume of this prism is the product of δl and the area of the projection of the element δs on the plane OYZ, i e

$$\delta l\,\delta s \cos\theta$$

As P_0 is equally likely to be at any point in the volume V, its chance of being in this prism of volume $\delta l\,\delta s \cos\theta$ is

$$\frac{\delta l\,\delta s \cos\theta}{V}$$

This is consequently the chance that the element δl of G intersects the surface element δs We may assume that δl is so small that the chance of intersecting the surface S more than once is negligible

Then the chance that δl intersects the surface S at some point is obtained by summing the chances of δl intersecting surface elements such as δs or by evaluating the integral

$$\int_s \frac{\delta l \cos\theta}{V}\, ds = \frac{\delta l}{V}\int_s \cos\theta\, ds,$$

taken over the surface S As the surface S is highly convoluted, and as the normals to the surface are equally likely to point in any direction, we have

$$\int_s \cos\theta\, ds = cS,$$

where c is the mean value of $\cos\theta$ To find c we consider a sphere centre O with unit radius The surface area of this sphere is 4π, the area of the projection of the surface on the plane OYZ is 2π (π from the hemisphere on one side of the plane OYZ and π from the hemisphere on the other side) The mean value for $\cos\theta$ is the ratio of these two areas Thus $c = \frac{1}{2}$, and the chance that the element δl intersects the surface S at some point is $\frac{S\delta l}{2V}$ On the average, the element δl will intersect the surface $S \frac{S\delta l}{2V}$ times So, summing over the whole length of the grid G, the grid will intersect the surface $S \frac{Sl}{2V}$ times on the average Although we have for convenience assumed that all the lines of G are parallel to the x-axis, it is clear that this assumption is not necessary This completes the proof '

Results of counts of intersections are recorded as n Since n varies directly with length of the grid or, which is the same thing, inversely with the cube root of changes in volume, a correction for shrinkage must be applied by dividing by the cube root of shrinkage of lung volume N therefore represents the slightly smaller number of intersections which would have been counted if lung volume had not shrunk during fixation To be comparable with results obtained by using other lengths of grid, results are calculated as $2N/l$, an estimate, as C A Rogers has shown, of internal surface area per unit volume of lung

RESULTS

Weight of the fixed lung

From tables 10 and 11 showing the loss of weight of the lung consequent upon fixation, a correction may be applied to weight of the fixed lung shown in table 13, in order to restore its loss

Density of the fixed lung

Density of the fixed lung was measured at four stages during the embryonic period Variation is probably the result of experimental error, and it is assumed that density of the fixed lung is a constant at 1 05 This is in some agreement with the statement of Faure-Fremiet & Dragoiu (1923), that in the sheep foetus it is of the order of unity

Volume of the fixed lung

Except in the few embryos where volume of the fixed lung was measured directly for the purpose of estimating density, volume in all other cases between the 18th and 28th days has been calculated from lung weight and density The mean figure from the data in table 16 can be corrected for shrinkage during fixation, and this is used as the basis for subsequent calculation

Table 13 Lung weight of the rabbit embryo

day		weight of fixed lung (g)		mean weight corrected for shrinkage (g)
18		(0.04)^{2}		0.04
20		(0.072)^{4}		0.072
23		(0.271)^{2}		0.271
24		0.33		
		0.335		
		0.455		
		0.275		
		0.347		
		0.418		
	mean	0.36	(+1.5%)	0.365
26		(0.74)^{7}		
		(0.94)^{5}		
		0.560		
		1.100		
		0.590		
		0.655		
		1.125		
		0.745		
		0.955		
		0.715		
		0.990		
		0.720		
		0.705		
		0.633		
		0.553		
		0.600		
		0.555		
		0.415		
		0.525		
		1.132		
		0.590		
		0.670		
		0.675		
	mean	0.656	(+8.5%)	0.715
28		1.021		
		1.008		
		1.065		
		0.778		
		0.885		
	mean	0.960	(+14.0%)	1.115
30		1.910		
		1.425		
		1.415		
		1.267		
		1.267		
		1.247		
		1.172		
		1.167		
		1.784		
		1.386		
		1.212		
		1.235		
		1.197		
		1.182		
		1.032		
		1.538		
		1.438		
		1.309		
		1.530		
		1.146		
		1.205		
	mean	1.335	(+15.5%)	1.58
31		0.980		
		0.955		
		0.990		
		0.980		
		0.870		
		1.055		
		1.385		
		1.355		
		1.550		
	mean	1.125	(+16%)	1.34

Figures for weight within brackets are mean values for the numbers of animals shown outside the bracket

Table 14 Density of the fixed lung Rabbit embryo

(From measurements made on the same lungs)

age (days)	mean weight of fixed lung (g)	mean volume of fixed lung (ml)	density of fixed lung
24 (3 lungs)	0.346	0.333	1.04
26 (5 lungs)	0.546	0.533	1.025
28 (5 lungs)	0.951	0.92	1.035
30 (3 lungs)	1.36	1.265	1.075
	1.29	1.2	1.07
	1.36	1.31	1.03
			mean 1.046

Experiments described earlier show that shrinkage of air-filled lungs by fixation *in situ* is probably negligible

TABLE 15 MEAN LUNG WEIGHT RABBIT EMBRYO, AND CALCULATED MEAN LUNG VOLUME

day	lung weight (g)	density = 1 05 calculated lung volume (ml)
18	0 040	0 038
20	0 072	0 068
21*	0 138	0 131
22*	0 204	0 194
23	0 271	0 258
24	0 365	0 347
26	0 715	0 680
28	1 115	1 100
30	1 580	1 500
31	1 340	1 275

* Values obtained by linear intrapolation between means

TABLE 16 MEASURED VOLUME OF THE FIXED LUNG RABBIT EMBRYO

day		volume of fixed lung (ml)		corrected lung volume (ml)
30		(1 200)[7] (1 310)[8]		
	mean	1 255	+14 8 %	1 47
31		1 0 0 8 1 0 1 3 1 3 1 5 1 5 1 2 1 4 1 4		
	mean	1 24	+15 2 %	1 46

These values are included with those of the preceding table in table 17

TABLE 17 MEAN LUNG VOLUME RABBIT EMBRYO

		lung volume (ml)		
day		direct measurement	by calculation	
18		—	0 038	
20		--	0 068	
21		—	0 131	
22		—	0 194	
23		—	0 258	
24		—	0 347	
26		—	0 68	
28		—	1 10	
30		1 5 1 47		
	mean	1 49	1 49	mean 1 426
31		1 275 1 46	— —	
	mean	1 375	1 367	

It will be noted from table 18 that the increase in lung volume during the first 24 hr following birth amounts to 40 % of lung volume before respiration has occurred

TABLE 18 VOLUME OF THE FIXED LUNG POST-NATAL PERIOD (RABBIT)

age	volume of fixed lung (ml)		age	volume of fixed lung (ml)
3 hr	1 9		48 hr	3 1
	1 1			2 5
	1 2			mean 2 8
	2 6			
	2 2		5 days	4 5
	mean 1 8			5 0
				4 5
4 hr	1 8			mean 4 66
6 hr	2 2			
	2 5		10 days	6 5
	1 7			7 0
	2 0			8 0
	2 5	mean = 1 956		mean 7 2
	mean 2 2		3 months	19 2
24 hr	1 35			21 3
	1 7			28 1
	1 9			mean 22 9
	2 0			
	2 1		adult	38 0
	2 6			46 4
	1 5			51 4
	2 1			47 2
	2 5			mean 45 75
	2 5			
	mean 2 025			

TABLE 19 PERCENTAGE COMPOSITION OF SECTIONS OF LUNG RABBIT EMBRYO

	measured to lumen (%)		measured to basement membranes (%)		
day	lumen	mean	lumen	mean	% occupied by epithelium
18 (2 foetuses)	5	5	10	13	8
	5		16		
21 (2 foetuses)	10	16	18	22	6
	22		26		
22 (3 foetuses)	17	22	27	33	11
	22		29		
	26		39		
24 (3 foetuses)	26	30	38	44	14
	28		41		
	35		49		
26 (4 foetuses)	34	44			
	41				
	46				
	57				
27 (3 foetuses)	42	50			
	52				
	58				
28 (3 foetuses)	45	51			
	56				
	54				
30 (3 foetuses)	54	57			
	56				
	61				

Growth of the respiratory lumen

The percentage area occupied by lumen (see table 19) as measured in a series of fields requires a correction for shrinkage, for it has been shown that the lumen shrinks whilst shrinkage of the interstitial tissues is negligible Since the extent of lumen is measured in terms of volume, the percentage loss of weight shown in table 11 requires to be divided by density and the quotient added to the figure for percentage of lumen This will involve recalculation, since the correct figure for the lumen added to that of the interstices must exceed 100 The percentages are recalculated from this total and the steps are indicated in table 20

TABLE 20 MEAN PERCENTAGE COMPOSITION OF SECTIONS OF LUNG EMBRYONIC PERIOD

day	percentage of lumen in fixed lung	percentage of interstices	percentage of lumen lost	percentage of lumen lost $\left(=\frac{\text{weight}}{1\ 05}\right)$
18	9	91	—	—
21	19	81	—	—
22	27 5	72 5	—	—
24	37	63	1 5 by weight	1 43 by volume
26	44	56	8 5 by weight	8 1 by volume
28	51	49	14 2 by weight	13 5 by volume
30	57	43	15 5 by weight	14 8 by volume

day	corrected % of lumen	percentage of interstices	total	true % lumen	true % interstices	total
18	9	91	100	9	91	100
21	19 00	81	100	19	81	100
22	27 50	72 5	100	27 5	72 5	100
24	38 43	63	101 43	37 4	62 6	100
26	52 10	56	108 1	48 2	51 8	100
28	64 50	49	113 5	57 0	43 0	100
30	71 80	43	114 8	62 7	37 3	100

TABLE 21 COMPOSITION OF LUNG VOLUME EMBRYONIC PERIOD

day	lung volume (ml)	volume of lumen (ml)	volume of interstices (ml)	$\frac{\text{lung volume*}}{\text{interstitial volume}}$
18	0 038	0 0034	0 0346	1 10
21	0 131	0 025	0 106	1 24
22	0 194	0 053	0 141	1 38
24	0 347	0 130	0 217	1 60
26	0 680	0 327	0 353	1 93
28	1 100	0 630	0 470	2 34
30	1 490	0 930	0 560	2 67

* This ratio is calculated here for later use when the principles underlying subdivision of the lumen are considered

Up to the 24th day, the presence of an easily visible epithelium must be taken into account when estimating the volume of lumen and of interstitial substance Owing to the great height of the epithelium in the early stages of development, the size of the lumen is often very small. It may be non-existent in the extremities of tubes Nevertheless, a luminal space will be defined by the basement membranes Two parallel sets of measurements have therefore been prepared, the difference between which represents the volume of epithelium

Between the 18th day of gestation and term, branching of the lumen occurs at a rate which exceeds that at which mesenchyme is being laid down Consequently the lumen enlarges until by term rather more than half the area of any lung field is occupied by lumen

TABLE 22 PERCENTAGE COMPOSITION OF LUNG POST-NATAL PERIOD

age	percentage of lumen	mean
1 day	65	68 6
	68	
	73	
2 days	68	76
	74	
	81	
5 days	76	80
	78	
	85	
10 days	82	85
	84	
	89	
3 months	83	88
	87	
	92	
adult (18 months)	88	90
	89	
	91	
	92	

TABLE 23 COMPOSITION OF LUNG VOLUME POST-NATAL PERIOD

age	lung volume (ml)	volume of lumen (ml)	volume of interstices (ml)	lung volume / interstitial volume
1 day	2 0	1 37	0 63	3 18
2 days	2 8	2 12	0 68	4 12
5 days	4 66	3 72	0 94	4 96
10 days	7 2	6 1	1 10	6 54
3 months	22 9	20 2	2 7	8 5
adult	45 75	41 18	4 57	10 0

Subdivision of the respiratory lumen foetal period

A series of lung fields, excluding so far as possible the larger structures and limited to the terminal portions of lobules, shows clearly the increasing complexity of branching of the respiratory tubes By drawing ten such fields on squared paper and by counting intersections of the drawing with the ruling, a quantitative estimate can be made of the internal surface area per unit volume ($2N/l$) of the lung or of total internal surface area ($2NV/l$) Before the 26th day, the presence of a complete epithelium interferes with the estimate No lumen will exist in the extremities of many tubes which are filled solid with epithelium On the other hand, a basement membrane is still present Two sets of data have therefore been prepared In the first, intersections with the basement membrane were counted In the second, only those septa have been counted which enclose a lumen however minute, and in this series the numbers of intersections are smaller than in the first After the 26th day epithelium now invisible by ordinary methods causes no further trouble It is to be noted that massive desquamation of epithelium occurs between the 24th and 26th days without influencing the slope of the line These data are shown in table 24

TABLE 24 SEPTA COUNTED PER UNIT AREA RABBIT EMBRYO

	counted to basement membrane				counted to lumen			
day	septa			mean	septa			mean
18 (2 foetuses)	20	26		30	18	16		18
	28	32			18	17		
	30	33			18	17		
	30	34			19	20		
	32	35			20	20		
21 (2 foetuses)	48	58		65	53	57		61
	56	60			60	58		
	62	74			63	62		
	68	78			63	63		
	70	79			66	63		
22 (3 foetuses)	83	74	87	89	69	70	72	79
	84	78	89		70	78	83	
	84	86	95		70	81	84	
	90	87	101		70	81	86	
	95	90	104		89	84	96	
24 (3 foetuses)	111	119	124	126	91	92	92	109
	116	122	125		97	98	106	
	118	126	130		105	106	115	
	124	131	136		106	117	126	
	126	132	138		127	124	128	
26 (3 foetuses)	135	120	118	137				
	136	130	130					
	144	140	133					
	149	146	134					
	151	146	140					
27 (2 foetuses)	118	169		158				
	120	177						
	131	178						
	139	188						
	154	202						
28 (2 foetuses)	174	173		177				
	174	173						
	174	174						
	175	186						
	180	185						
30 (2 foetuses)	198	198		208				
	199	209						
	201	220						
	206	221						
	218	224						

From embryonic material these counts will require correction for shrinkage due to fixation It is clear that too many intersections have been counted, since the area of lung has shrunk in proportion to the shrinkage of lung volume Since the numbers of intersections are proportional to grid length, the counted number divided by the cube root of volume lost by shrinkage will reduce the counts of intersections to the extent required by the same lung field in which no shrinkage had occurred This correction has been applied in table 25

Subdivision of the respiratory lumen birth and neo-natal period

During the first 24 hr following birth, the effects of aeration show an irregular distribution in the lung Certain lobules contain no air and may be collapsed, others are well expanded Depending upon the extent of collapse, the aerated lobules are often over-

TABLE 25 NUMBERS OF SEPTA (BETWEEN THE 18TH AND 24TH DAYS MEANS OF BOTH VALUES ARE SHOWN)

day	septa counted ($=n$)	$\sqrt[3]{}$(shrinkage) (see table 11)	corrected for shrinkage ($=N$)	$2N/l$
18	24	—	—	87
21	63	—	—	227
22	84	—	—	302
24	117	1 005	116	418
26	137	1 013	135	485
28	177	1 033	172	620
30	208	1 04	200	720

distended, an effect which slowly disappears as more and more lobules expand It is, in my experience, uncommon to see a lung in which aeration is uniform during the first 24 hr

At 48 hr, aeration is uniform Spaces previously over-distended, compressing the adjacent architecture, are now represented by regularly spaced ducts in whose septa a remarkable change has occurred Septa everywhere are now minutely indented and show numerous small septa drawn up between the indentations The expansile stress of respiration, originally merely distensive, has become redistributed to produce regular indentations of the septa as a result of increase of tension in the elastic fibres in their free edges The walls of the alveolar ducts thus become minutely honeycombed by new formation of polyhedral chambers (the alveoli) whose septa are drawn up by elastic fibres into the lumen of the alveolar duct This is a very different process from an expansile formation of alveoli by budding from the alveolar duct, budding must occur into interstitial tissue, and such a mechanism would require a far larger amount of interstitial tissue than actually exists in the lung before this stage is reached

In consequence the pattern of lung architecture shows the first post-natal signs of increasing subdivision The subdivisions are smaller than have been seen in the earlier stages and gradually exhibit a very clear pattern within the lobule, being situated as a double row on each side of the septa between adjacent alveolar ducts There is no objection to calling these subdivisions 'alveoli', providing it is realized that the alveolus of one stage is destined to become the alveoli of the next The size of the smallest subdivisions at term is the same as that at 10 days of life, and when it is remembered that lung volume has been multiplied 7 times, it is obvious that there is no foetal homologue for the 10-day alveolus

Some attempt can be made to decide how far the formation of septa depends upon vital processes of growth and how far upon the purely mechanical effects of distension by increasing tension in elastic fibres The possibility that active contraction of plain muscle in the free edges of alveolar ducts may play a part in determining lung architecture may be considered, though it is difficult to investigate further The results of artificial distension of an excised lung, however, will not depend upon vital processes, and may be expected to intensify the effects produced by increase of fibre tension

It is found that artificial distension of the excised lung at term reproduces the picture of the normal lung at 5 days after birth The mean cross-sectional area of the smallest spaces in the distended lung is smaller than those in the undistended lung (see figure 41) The effect of distension upon the excised lung at term is therefore to subdivide existing spaces by drawing up new septal divisions. Yet evidence of distension is seen in the longer and wider alveolar ducts and in the larger lobules Parallel with these changes, the effect of distension is to produce a marked narrowing of the septa Stretching cannot account for all of it, part is due to a redistribution of the capillary bed within the newly formed septa, and this has already been described

By applying the method for estimating internal surface area per unit volume of lung ($2N/l$), it is seen in table 26 that the effect of respiration for 24 hr is to reduce the numbers of intersections with the ruling This is due mainly to enlargement of the septal mesh Though a few existing septa may be flattened by hyperdistension, the numbers of septa cannot be seriously reduced By dividing the numbers of septa at term ($N=200$) by the

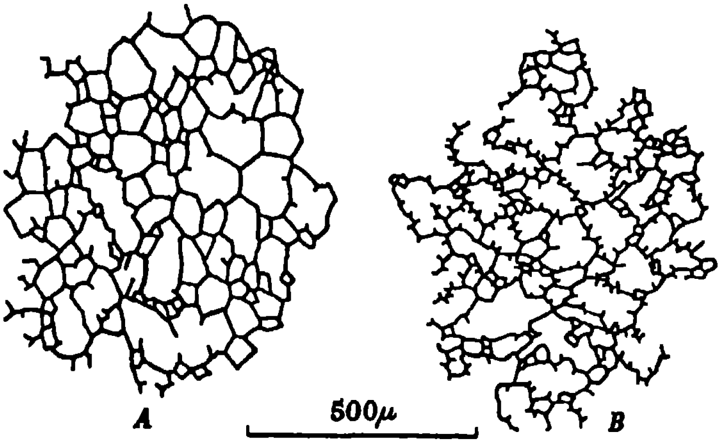

FIGURE 41 Effect of artificial distension upon the size of the smallest subdivisions in a pair of lungs, 2 days after birth *A*, natural size, *B*, distended

cube root of the enlargement of lung volume ($\sqrt[3]{(1\ 4)}=1\ 12$) which has occurred by 24 hr respiration, an estimate may be made of the pattern at term subjected to distension The result, $N=179$, is in tolerably good agreement with the figure for 24 hr ($N=164$) However, many lobules remain collapsed, and the whole picture is so varied that quantitative estimates can only be made in those parts where reasonably uniform conditions are present Results for the post-natal period are shown in table 26

By 48 hr, in spite of the fact that lung volume has increased, the number of intersections is of the same order as the figure at term By 5 days it is exceeded and more so by the 10th day When it is remembered that lung volume was increased by a factor of almost 2 at 48 hr, by 3 2 at 5 days and by 5 at the 10th day, it is obvious that considerable new formation of septa is taking place It would otherwise be impossible for the counted number of intersections to increase, for unless the pattern changes, distension of the septal mesh by respiration must of necessity reduce the numbers of intersections, in proportion to the cube root of the increase of lung volume

At some time between the 10th day and 3rd month of the rabbit's life, the formation of septa ceases The counts of septa therefore fall slowly as the result of distension by growth of the existing lung architecture By dividing the counts from term onwards by the cube roo of increase in volume at the same times an estimate may be made of the resulting complexity when the original pattern is subjected to simple distension by growth and enlargement of the thoracic cavity Results of such calculation are shown in table 27

TABLE 26 COUNTS OF SEPTA—POST-NATAL PERIOD

age	septa counted			mean (= N)	$2N/l$
24 hr	128	149	151	164	590
	129	152	159		
	131	178	168		
	154	197	178		
	186	200	200		
48 hr	161	194	203	211	760
	178	198	218		
	183	224	231		
	198	228	246		
	200	245	247		
5 days	213	214	217	245	880
	220	230	227		
	222	249	251		
	231	264	253		
	237	269	275		
10 days	243	254	249	259	935
	250	257	266		
	250	259	268		
	261	260	270		
	286	261	272		
3 months	179	188	198	200	720
	184	197	201		
	190	200	212		
	195	208	217		
	198	211	222		
adult	119	121	134	140	503
	125	130	145		
	128	137	154		
	139	146	159		
	149	148	167		

TABLE 27 POST-NATAL GROWTH OF THE LUNG

age	lung volume (ml)	ratio increase	cube root of increase	septa (N)	$\frac{N \text{ of previous stage}}{\sqrt[3]{\text{(increase)}}}$
term	1 49	1	1	200	—
10 days	7 2	4 85	1 69	259	118
3 months	23	3 2	1 47	200	176
adult	46	2	1 26	140	159

If, therefore, the lung at term ($N=200$) is distended without altering the pattern of architecture, 118 intersections would be found Actually 259 are counted Septa have therefore been formed If the 10-day lung is distended to the volume at 3 months 176 septa would be counted Actually 200 are counted, but the standard deviation of the order of ± 20 shows that the estimated count is probably the same as that actually found It would therefore appear likely that alteration in pattern of lung architecture had been accomplished by the 10th day of the rabbit's life Thereafter distension enlarges the pattern, and it is found that the pattern at 3 months ($N=200$) subjected to distension yields a result ($N=159$) not significantly different from that actually found ($N=140$)

Elastic fibres

Though essentially histological, this section has a close relation with the quantitative data under consideration The position of the inter-duct or inter-alveolar septa is seen to depend entirely upon the distribution of elastic fibres One or more elastic fibres are present in the free edges of all septa, however small they may be The rule is invariable and applies to embryo and to the adult It is also interesting that the numbers of elastic fibres appear to be increased as a result of expansion of the lung by respiration at birth

Owing to the weak staining properties of elastic fibres in the embryo, their distribution is not so easy to determine as it is in the adult The larger bundles are situated in the free edges of the alveolar ducts Smaller fibres encircle the walls of the ducts, producing a slight constriction of the lumen, but owing to their weak staining properties it may be difficult to trace their relation to adjacent ducts or to trace the complete circle Such is the arrangement at term 48 hr of respiration produces striking changes both in the staining qualities and, apparently, in the amount of elastic tissue which appears to have increased considerably

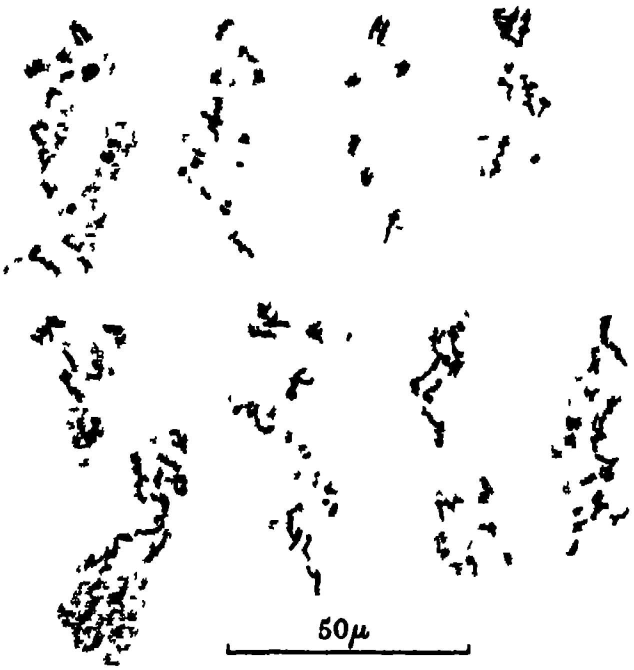

FIGURE 42 Comparison of numbers of elastic fibres in septa of comparable size in normal sized (upper row) and distended lungs (lower row) Rabbit foetus at term

The increased subdivision and angularity of the alveolar ducts has evidently been evoked by a parallel response in the numbers of elastic fibres The main strands sweep round the alveolar ducts at regular intervals, drawing up folds into the lumen, as may be seen by looking into the mouth of an alveolar duct in a thick section Respiration has stretched the fibre and distorted the unresisting, probably inelastic, reticulum scaffold of the alveolar walls A fold is thus formed by the elastic fibre in its free edge The pictures of Orsos (1907, 1933, 1936) show how the reticulum framework of the septum is braced on to the elastic fibres by a splicing of fine reticulum fibres Between these folds the alveolus, as it were, spreads sail and the pressure of adjacent lumina may impress a faceted contour

An exactly parallel effect can be produced by inflation with air or with formalin in excised foetal lungs at term Figure 42 shows that a larger number of elastic fibres is present in the distended lung Most of this effect is probably due to splitting and separation of fibres from the main bundles, of which more appear thicker in the undistended lung and become thinner and more numerous after distension I cannot convince myself that stretching (whether by respiration or by artificial distension) produces any enhancement of staining either by resorcin-fuchsin or by orcein It is preferable to attribute the effect to splitting, and it may be that the lapse of 48 hr before subdivision of alveolar ducts occurs is due to the time required for splitting of the main bundles The purely distensive effect at 24 hr is therefore to stretch the main bundles, subdivision of the lumen at 48 hr is the result of redistribution of tension by thinner fibres split from the main bundles

The minute arrangement of fibres at the points where bundles appear to cross suggests how increase of tension will evoke a new septum and permit also of further formation of septa At such points, close examination shows that many fibres do not cross (see figure 43) Opposite limbs of one loop are arranged so as to separate in the same direction when tension is applied The space between two such loops forms the anlage of the alveolus of the next generation At such places, rudiments of two or three future generations of alveoli may be recognized It may be assumed that new formation of alveoli stops when the disposition of elastic fibres no longer permits of their splitting to form a new series of spaces When this occurs, further growth of the thorax is accompanied by dilatation without subdivision of existing alveoli, but other evidence from the rat (Hilber 1934) and the dog (Longacre & Johansman 1940) suggests that species differences are of great importance in deciding when new formation of septa ceases

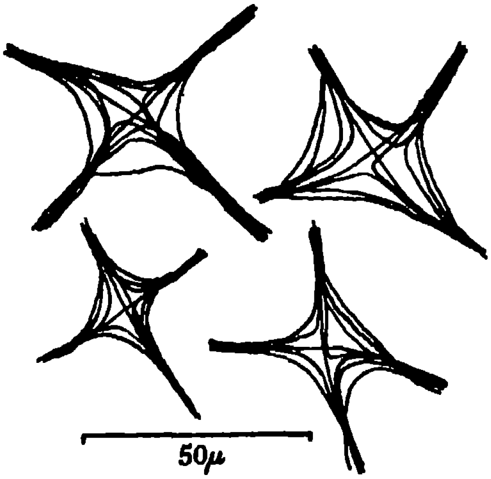

FIGURE 43 Arrangement of elastic fibres at points where bundles appear to cross Rabbit at term

The weak staining properties and late appearance of elastic fibres in the foetus have been noted by Lenzi (1898), Linser (1900) and by Dubreuil, Lacoste & Raymond (1936), who described their earliest appearance in the walls of the pulmonary artery Following birth, its improved staining qualities were regarded by Ottolenghi (1903) as the result of contact with air and therefore as having an application to forensic medicine His results in man were re-examined by Ogawa (1920) in the rabbit, who was unable to satisfy himself of any significant alteration in staining at birth However, a similar conception seems to have been held by Keibel & Mall (1912), who write that 'The tissue [elastic fibres] does not stain as deeply as it does later on and is to be regarded as young, immature elastic tissue which becomes mature a few weeks after birth as the result of use' Foerster (1932) and Bohmer (1933) consider that staining is improved by birth Policard (1938) remarks that 'La mise en fonctionnement de ces fibres [elastiques] sous l'influence de la respiration aerienne, modifie probablement leur constitution colloidale intime ' It is therefore a matter for regret that the present investigation does not support the view that the staining of elastic fibres depends upon their having been stretched

PRINCIPLES OF SUBDIVISION OF THE LUNG LUMEN

Superficial inspection of a series of lung fields from the later stages of embryonic life would appear to show an increase of lumen at the expense of the surrounding mesenchyme Measurement, on the other hand, suggests that mesenchyme increases in order to provide a mantle for a lumen which is becoming more and more complex, to provide, in Goodrich's (1930) phrase, 'the building material for future differentiation' In this section, the principles are examined which underlie this differentiation

The force required to produce an enlargement of lung volume increases with the number of elastic fibres and therefore with the tension evoked by stretching them Though there are no quantitative data concerning numbers of elastic fibres, it is clear that they increase as the numbers of septa increase both before and after birth It is also clear that both elastic fibres and septa increase, whilst the percentage of interstitial substance continually decreases Hence the number of elastic fibres increases with the reciprocal of the percentage of interstitial volume, i e with the ratio of lung volume to interstitial volume Probably the fibre tension also increases with this ratio The increasing values of the ratio of lung volume to interstitial volume in table 28 show that lung volume increases more rapidly than interstitial volume both before and after birth Since the interstices contain elastic fibres the effect of this inequality of growth rates may be to stretch these fibres Tension is thus maintained in elastic fibres, and it is this factor which is here regarded as underlying the formation of septa and which itself may be a consequence of the unequal rates of growth of lung volume and interstitial volume If it is possible to show that a simple relationship exists between the numbers of septa ($2N/l$) and the values of the ratio, some evidence of a causal relation between fibre tension and septa will have been obtained

TABLE 28 DATA FOR FIGURE 44

age	lung volume / interstitial volume (from tables 21, 23)	counts of septa = $2N/l$ (from tables 25, 26)
18 days	1 1	87
21 days	1 24	227
22 days	1 38	302
24 days	1 6	418
26 days	1 93	485
28 days	2 34	620
30 days	2 67	720
birth		
1 day	3 18	590
2 days	4 12	760
5 days	4 96	880
10 days	6 54	935
3 months	8 5	720
adult	10 0	503

In figure 44 the values for the ratio of lung volume to interstitial volume are plotted against septa *($2N/l$)* *The graphical relationship is linear, though the slope changes three times between embryonic and adult life The four periods so defined may be considered in turn*

The first period ends with the first signs of desquamation of 'alveolar' epithelium This can be recognized at the 24th day in the rabbit During this period more subdivision of the lumen takes place for a given increase in the ratio than is found at any subsequent period

The second period starts with desquamation of epithelium and ends at birth The slowing of subdivision for a given increase in the ratio may be the result of desquamation of epithelium, but it is difficult to see how desquamation of epithelium affects the issue one way or the other Having in mind the experiment by which subdivision of the lumen was accomplished by simple inflation of an excised lung, the effect of epithelium upon subdivision under these circumstances can clearly be dismissed Its desquamation, moreover, cannot be interpreted as removal of a factor which hampers the growth of lung volume, lung volume shows signs of a slower rate of growth after the 26th day On the other hand, the slowing may be another effect of the cause which also promotes desquamation During this period the ratio increases more rapidly than subdivision Increase in the ratio may be the result either of a relative increase in lung volume or of a relative decrease in interstitial volume It seems possible to separate these two factors by plotting the ratio against its numerator and denominator separately This has been done in figure 45, which shows that an increase in the ratio during the first period is associated with almost as much increase of interstitial volume as of lung volume In the second period (after the 24th day), on the other hand, increase in the ratio is accompanied by marked slowing in interstitial volume as compared with the total volume of the lung

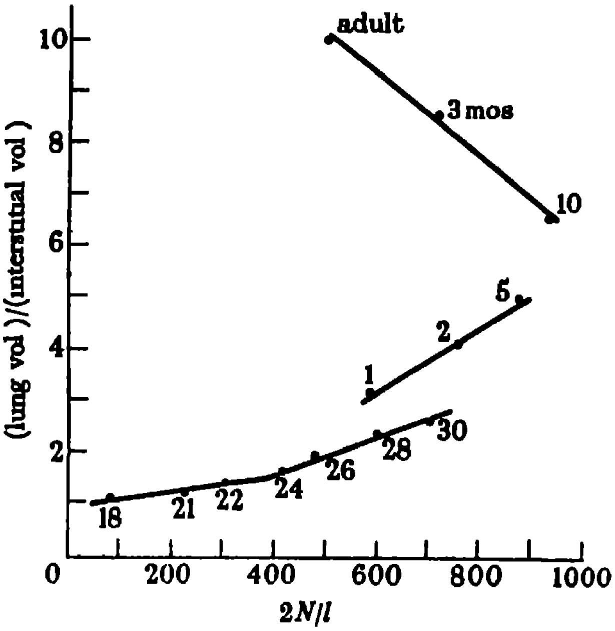

FIGURE 44 Linear relation between the ratio of lung volume to interstitial volume and $2N/l$ Four phases with characteristic slopes are seen (see table 28)

It is therefore probable that desquamation of epithelium is the earliest manifestation of the factor by which growth of the interstitial tissues of the lung is slowed This factor may well be fibrinolysis, direct evidence for the existence of which was found in tissue culture of foetal lungs by Carleton (1925) It has already been pointed out in the histogenesis of the respiratory epithelium that the reticulum basement membranes disappear when the epithelium desquamates

The third period commences with birth The initiation of respiration causes a greater increase in lung volume than in volume of the interstitial tissues Consequently the slope changes though the trend remains linear During this phase, which probably lasts as long as 10 days, considerable increase in complexity of subdivisions of the lumen is found

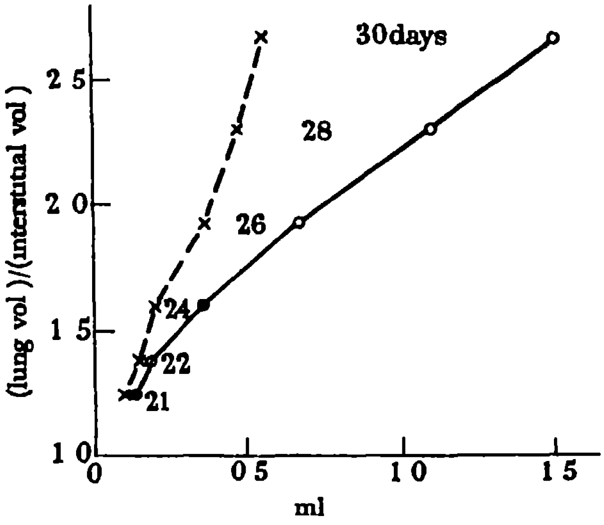

Figure 45 For explanation see text ——, lung volume, – – –, interstitial volume

During the fourth or terminal phase, increase in lung volume is no longer accompanied by subdivision, and in consequence the existing lung architecture is subjected to simple distension by growth of the whole organ The trend is still linear but its direction has become re-entrant

A simple relation has been demonstrated between numbers of septa ($2N/l$) and the ratio of lung volume to interstitial volume, but it must be remembered that graphical relationship, however suggestive it may be, is not proof of a causal relationship However, when one factor may be equivalent to tension and the other is septa with elastic fibres in their free edges, the suggestion of causal relationship is undeniably strong

This method of growth postulated for the Amphibia by Marcus (1928), Heiss (1923), for certain Mammalia by Hilber (1934) and Willson (1928), is the result of subdivision of space by centripetal formation of septa In the amphibian or reptilian lung, the free edges of the septa, in addition to elastic fibres, contain large muscle bundles (Oppel 1905, Schultze 1871), no doubt capable of exerting traction on the septum to increase or diminish the area of capillary bed according to the demand It will make no difference to the argument whether a positive pressure exists within the lung lumen to distend the lung (as in Amphibia) or whether the lumen is enlarged by pressures lower than atmospheric outside the lung (as in Mammalia) Both mechanisms will evoke elastic recoil, assisted in Amphibia by contraction of plain muscle in the edges of the septa Available evidence shows that the facts of lung growth in the rabbit can be fitted more easily into this scheme than into the alternative scheme of alveolar budding supported by Bremer (1935) Whether or not the desquamation of epithelium from the distal portion of the respiratory tree be accepted as a fact (and strong evidence has been produced to show that this occurs in the foetus and persists in the adult), epithelial growth cannot account for the quantitative facts of growth of the lung lumen and its subdivision Nor can it account for the fact that the structure of a 5-day-old lung can be reproduced by simple inflation of one that has never breathed

One further step can be taken The number of septa is clearly a function of internal surface area of the lung which is therefore a linear function of the rates of growth of lung volume and interstitial volume This relation expresses ‘the phenomenon which is visible throughout the whole field of morphology the tendency (referable doubtless in each case to some definite physical cause) for mere bodily surface to keep pace with volume, through some alteration of its form’ Illustrating this principle with cases of organs furnished with complicated luminal subdivision, D’Arcy Thompson (1942) proceeds ‘the vast increase in respiratory surface in the air sacs and alveoli of the lung, all these and more are cases in which a more or less constant ratio tends to be maintained between mass and surface, which ratio would have been more and more departed from with increasing size, had it not been for such alteration in surface form’

The total internal surface area of the rabbit’s lung can be calculated from the formula $2NV/l$, and its ratio with body weight is shown for the span of the rabbit’s life in table 29 Except for the earliest period of growth and for the period of maximum evocation of septa after birth, the ratio is probably to be regarded as a constant

TABLE 29 LUNG SURFACE-BODY WEIGHT RATIO

age	$2N/l$	lung volume (ml)	area of internal surface of lung $=2NV/l$ (sq cm)	body weight (g)	$\frac{\text{internal surface}}{\text{body weight}}$
18 days	87	0 038	3 3	1 5	2 2
21 days	227	0 131	29 7	4	7 42
22 days	302	0 194	58 7	5	11 7
24 days	418	0 347	145	13	11 2
26 days	485	0 68	328	25	13 1
28 days	620	1 10	680	40	17 0
30 days (birth)	720	1 49	1,040	54	19 2
1 day	590	2 0	1,180	50	23 6
2 days	760	2 8	2,120	80	26 6
10 days	930	7 2	6,700	140	48
3 months	720	22 9	16,400	900	18 2
adult	500	46 0	23,000	1,500	15 3

It is interesting that D’Arcy Thompson speaks of ‘some definite physical cause’, in the lung there is evidence of the importance of tension in elastic fibres, shown most clearly when the lung starts to breathe but apparently in existence during intra-uterine life

I am indebted for technical assistance and advice to Mr J H Bayley and Mr F Crew of University College Hospital Medical School I have sought to draw many friends into discussion of difficult points, and in particular I would mention Drs L E Glynn, K K Cheng, F A Denz and D A Sholl, the latter of the Department of Anatomy, University College As explained earlier, the mathematical interpretation of certain measurements in part 2 is due to Mr C A Rogers of the Department of Mathematics, University College, London. To Professor G R de Beer, F R S , I am indebted for much advice, and to Professor G R Cameron, F R S , for help and guidance through fields far wider than are represented here Expenses were met by a grant from the Graham Research Fund of the University of London

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Description of plate 1

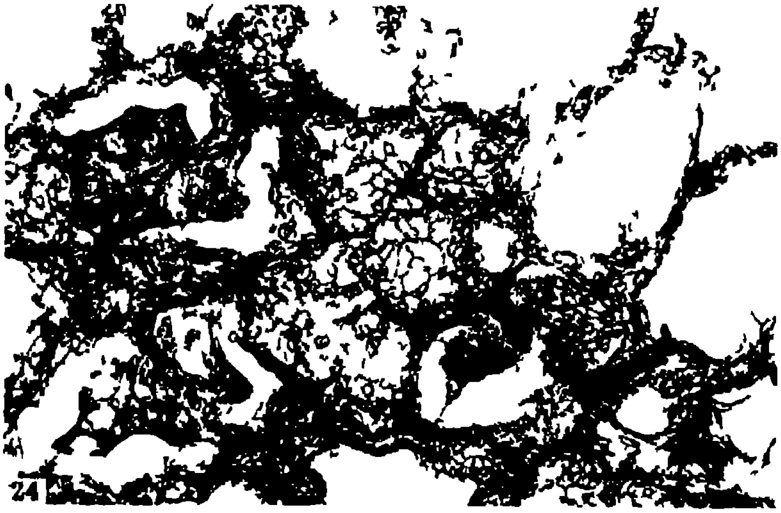
Figures 24, 25 Silver impregnation of lung (? kitten) by Gustav Mann, from a preparation in the Department of Histology, Oxford University (by permission of Dr H M Carleton) Magn × 63, × 77

Figure 30 Traces of impregnation of epithelium in subpleural alveolus Adult rabbit Magn × 800

Figures 31, 32 Traces of impregnation of epithelium in alveoli adjacent to pulmonary artery Note the cement lines crossing the intercapillary spaces and a small nucleated cell in figure 32 Adult rabbit Magn × 800

Figures 35, 36, 37 Dissociation of alveolar septa produced by perfusion of fixative The absence of epithelial nuclei and the presence of a delicate surface membrane are to be noted Adult rabbit Magn × 530

Figure 38 The point of termination of bronchiolar epithelium from the same preparation Distally, only the delicate membrane is seen Adult rabbit Magn × 530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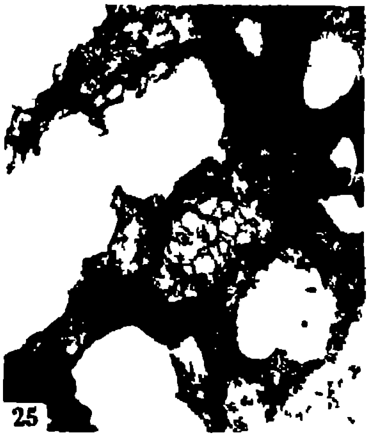
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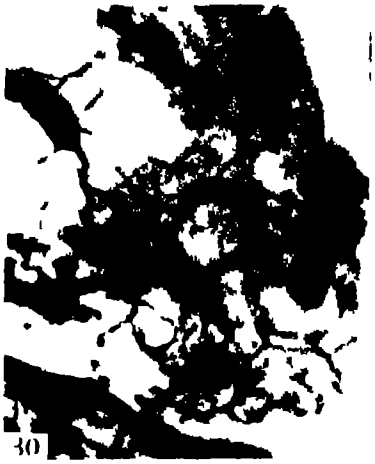
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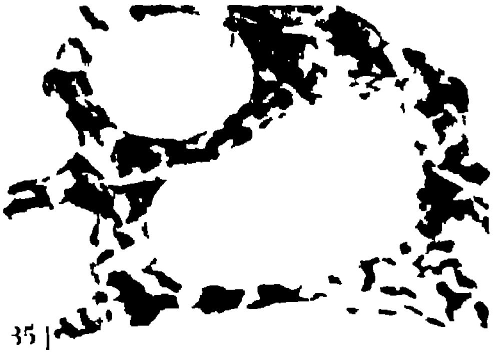
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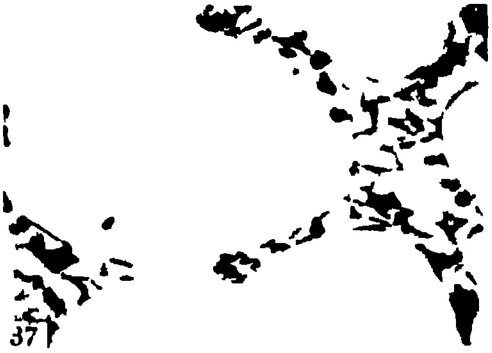
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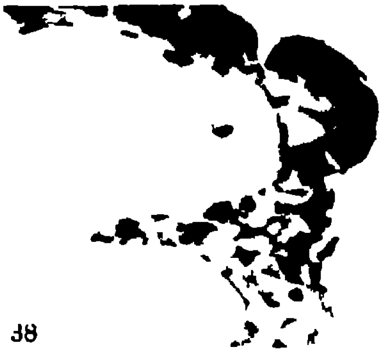
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EARLY PALAEOZOIC STARFISH

BY W. K. SPENCER, D.Sc., F.R.S.

(*Received* 25 *February* 1950)

[Plates 2 to 8]

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The fossil starfish described here are mainly from the Lower Ordovician (including the Tremadocian). Only brief descriptions of these starfish have been given previously. They are the earliest starfish known, and arrived in a series of transgressions which began in the Tremadocian and persisted throughout the immediately succeeding beds. Each of the transgressions brought in new faunas. Cephalopods arrived in the Tremadocian and locally graptolites in the basal Arenig.

The grouping of the starfish adopted here is based upon the activities of the arms, especially during feeding. Three groups of starfish are recognized. Two of these groups are recognizable as Asteroidea and Ophiuroidea. In both these groups the arms are functional, but the arm activities have different mechanisms.

The asteroid arm from the beginning is adapted for a carnivorous diet of large food, whilst the arm of the primitive ophiuroid is adapted for feeding on the small food present in or near the sea bottom. It is suggested that the primitive Ophiuroidea, like the recent *Amphiura*, had a 'burrowing habit'.

The third group had no functional arms. The forms belonging to this group appear slightly earlier (Tremadocian) than do either the Asteroidea (Lower Arenig) or the Ophiuroidea (basal Arenig). The tube feet are placed in position by changes in body shape. They seem to have lived on small food either from the planktonic shower (*Villebrunaster* n. g.) or from that in the upper layers of the bottom (*Archegonaster*). Their skeleton shows many primitive characters. The name Somasteroidea n. subclass is suggested for this third group. Its members show the first stages in the differentiation of a starfish

[Published 16 January 1951

It is noticeable that these first stages show no sign of an ambulacral groove, a character which previously has been regarded as primitive and used to link starfish with certain non-crinoid Pelmatozoa (Edrioasteroidea Bather, Thecoidea Jaekel)

The view held (Spencer 1905) that the asteroid groove was present in early Echinoidea must also be abandoned

Early representatives of all these groups have characters which link them with a common ancestral structure Each tube foot is housed on two ambulacralia in all Asteroidea (living and fossil), in the Somasteroidea and in the extinct primitive Ophiuroidea Some groups of Ophiuroidea retain this character throughout the early Palaeozoic, whilst other groups acquired 'vertebrae' Each vertebra, a modified ambulacral, acquires its own tube foot All early representatives have a mouth frame with radial V's It is suggested that the presence of the V's is associated with a primitive oral opening, the stomodaeum, which had radial slits, the buccal slits *

The Somasteroidea have an aboral skeleton composed of ossicles which are little more than spicules radiating from a number of centres The arrangement can be compared to that in the early stages of the skeletal components of recent forms No other fossil echinoderm is known with ossicle components in a condition as primitive as this

It would seem that starfish arose at a very early stage in the development of echinoderm stocks

INTRODUCTION AND HISTORICAL

The interrelationship of the two great groups of starfish, the Asteroidea and the Ophiuroidea, was firmly established by Ludwig many years ago Applying the principles of comparative anatomy he showed that both were built to a common plan, and turning to embryology he found an asteroid stage during the development of the ophiurid

The prestige of Ludwig and the clarity of his observations have profoundly influenced palaeontologists Schuchert, who wrote the first clear account of the evolution of the Palaeozoic Asteroidea, found an archetype to both groups in the primitive asteroid *Hudsonaster*, which (1915, p 34) he held to 'be very near the radicle that gave rise through modification and inheritance to all subsequent Stelleroidea' His diagrams show that he regarded the arrangement of the plates of the dorsal surface of the disk as closely resembling those of a crinoid

Both Jaekel and Bather looked for the asteroid ancestry in another Pelmatozoan group, the Edrioasteroidea of Bather, the Thecoidea of Jaekel The asteroid character regarded as primitive was the open ambulacral groove with its floor of double plates and its wall of cover plates (adambulacralia) (see p 121) An endeavour was also made (Spencer 1904) to apply this 'groove' theory to the establishment of the relationship between Asteroidea and Echinoidea

The observations given below throw suspicion upon the above views They are based largely upon new material from the south of France, which was shortly described by Thoral (1935) in his comprehensive survey of the fossil fauna found in the Tremadocian and basal Arenig in the neighbourhood of St Chinian Several groups of animals, including the starfish, make their first appearance in the European rocks during this period, and no earlier starfish have been found anywhere

Dr Stubblefield put me in touch with Professor Thoral, who on learning of my interest in the starfish, proceeded to give me every help He lent me material and gave me facilities to work in his Department in the University of Montpellier I am very grateful to him for this and for much pleasant companionship

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* For definition see Glossary, p 124

My second source of material for studies upon early starfish is a large collection from the Upper Arenig of Bohemia This fauna was thoroughly examined by Jaekel, who published two short papers Neither described the genera in detail, but the latter paper stated his general views upon the place the genera should occupy in classification It was later arranged that he and I should collaborate in a full description, but his untimely death prevented this The manuscript notes forwarded to me elaborate his views and give accurate descriptions, with illustrations of many of the genera I am not following Jaekel's viewpoint exactly I feel that he himself would have modified it if he had been acquainted with the earlier French fauna This material has been in my hands rather a long time, and the patience of those who control the Narodni Museum, Prague, must have been somewhat tried Without it my work would have been seriously hampered, for it has taken me several years and much study to understand the implications of the fauna

It now seems possible to draw some general conclusions which are briefly

(1) That the earliest known starfish are found in Western Europe They arrived in a series of floodings which brought in the Tremadocian and Lower Arenig faunas

(2) That starfish unmistakably, like recent Asteroidea and Ophiuroidea, arrived in the Lower Arenig Both show certain primitive characters Those possessed by the Ophiuroidea are of special interest, for they show the arm structure prior to the modification of the ambulacralia into vertebrae

(3) That these early faunas contain a third group, called here the Somasteroidea n subclass In this group the arms are in an early stage of differentiation This group arrived in the first, Tremadocian, floodings The manner of differentiation is not in accordance with the view that a 'groove' structure is of importance in an assessment of ancestral characters

I am greatly indebted to Dr Barnard for the facilities afforded me at the South African Museum and to Mrs Mary Maytham Kidd for her clear illustrations The completion of this communication would have been very difficult without their help I am also indebted to Dr C J Stubblefield for assistance in the preparation of the manuscript, to Professor Day of the University of Cape Town, to Lady Rutherford for rescuing both material and drawings which in 1941 had to be abandoned in France and to the British Museum (Nat Hist), Geological Department, for assistance at all times

Material

The starfish, both in the French and Bohemian beds, are found by splitting rounded flint-like nodules which are often found loose in weathered soil I accompanied Professor Thoral on some of his collecting expeditions In particular, we visited vineyards where the soil, kept in a constant state of cultivation, was a source of much material Usually the owner of the vineyard had put aside a heap of nodules exposed during his cultivation Other nodules were found during the visit by stirring the soil with a suitable geological hammer A very large proportion of the nodules when split showed that the 'flint' had formed around an animal nucleus

Starfish form only a very small proportion of the fossils collected in this way, and the material available for study is the result of collection over many years The part played by the individuals who were interested in collecting for its own sake cannot be overestimated

All the fossils are preserved as moulds It is usual to find only portions of the body of the starfish within the nodule, but these portions are very perfect Casts from the mould show fine details, spines, joints and facets for the accompanying musculature, grooves for vessels, in fact all the information which can be obtained from a well-preserved endoskeleton

The explanation which seems to fit the observations on the material is that the portions preserved were within the mud of the sea-bottom at the time of death, and that chemical interaction between the animal matter and the surrounding mud caused the enclosure of the remains in a 'flint' casing During this interaction the calcite of the skeleton was gradually dissolved away Possibly compounds of iron entered into this reaction Usually the hollow of the moulds is filled in with a ferric oxide or carbonate, sometimes so hard that it has to be removed by a needle before a cast is made

The proportion of the original animal preserved varies considerably according to its build Generally speaking, we can say that the central parts are often preserved in their entirety, whilst the projecting parts, the arms, are often missing It is suggested later that some, if not all of these starfish, had a burrowing habit The parts of the starfish which were well preserved were those in the deeper parts of the burrow The portions badly preserved or absent were thrust upwards into the top layers of the bottom mud, to feed from the layers richest in organic remains

The following studies endeavour to interrelate studies of preservation with studies of the structure of the individual ossicles Such studies seem to make possible a reconstruction of the habits and trends of evolution of these early starfish

Feeding habit

Hunt (1925) suggested the following classification of feeding habit

A *Suspension-feeders* appertaining to animals 'either permanently sedentary in habit or at least remaining in one place when feeding They feed by creating currents of water over parts specialized to strain or select from the water its contained small floating particles and organisms '

B *Deposit-feeders* These include *selective feeders*, animals which pick out organic material from the substratum by a variety of prehensile devices

C *Carnivores* Animals which specialize in the capture of prey, other living animals, or in some cases carrion

Respiration

Gemmill (1915) showed that respiratory ciliary currents, both ectodermal and endodermal, washed large areas of the parts of the asteroid body, and that the path of these currents could be traced by examination of the body surfaces

Respiration in the Ophiuroidea is confined to limited areas, respiratory pouches (sometimes called genital bursae) These pouches are formed during body outgrowths (the ophiuroid disk)

Classification

The classification adopted is linked with the above observations on habit It seems to satisfy studies upon the palaeontological material, whilst offering the least disturbance to groupings familiar in literature

Subclass Somasteroidea nov (diagnostic characters, see below)

This new subclass includes a number of very early starfish in which the arms are just beginning to be differentiated There is evidence that at least one form, *Villebrunaster* n g, was a suspension-feeder This mode of feeding connects with a probably ciliary feeding pelmatozoan ancestor

Subclass Asteroidea (diagnostic characters, p 121)

Carnivorous starfish with well-developed stout arms The structure of the skeleton of the arms is linked with the habit of engulfing its food in an everted stomach

Respiration both ectodermal and endodermal Many forms have external gills (papulae)

Subclass Ophiuroidea (diagnostic characters, p 106)

The primitive Ophiuroidea, like many of the recent forms, were selective deposit-feeders Both the long thin arms and the modification of the proximal tube into buccal tentacles are well adapted for this mode of feeding Carnivorous Ophiuroidea evolve later Their very mobile arm, used in the capture of food, is highly specialized

Respiration from the outset was by means of respiratory pouches developed between the edge of the disk and the arms This method of respiration is peculiar to the Ophiuroidea

Subclass SOMASTEROIDEA n subclass

Diagnostic characters

The central part of the body is large and the 'arms' are merely differentiated portions of its oral surface In the earliest genera the skeleton of this surface has only two types of ossicles (1) ambulacralia, arranged in a double alternating row which stretches from the central opening to an arm extremity, and (2) interambulacralia, rod-shaped ossicles placed in linear series at an angle to the ambulacralia In the Upper Arenig genus *Archegonaster* marginalia and adambulacralia are differentiated as end-members of these interambulacral rows In still later genera the interambulacral skeleton is entirely wanting

The aboral skeleton, when present, has ossicles with a small centre from which radiate slender branches The whole forms a net with a wide mesh

This subclass contains only a few genera, but they are important as they include the earliest known starfish and show peculiarities of skeletal build which do not find a parallel in either Asteroidea or Ophiuroidea The general plan of such a skeleton is well shown in figure 1, founded upon well-preserved specimens of *Villebrunaster* n g

The interambulacralia are especially characteristic The rods are walls of shallow channels Such ossicles are only found in members of this subclass They are called virgalia* in the following descriptions

The ambulacralia are also characteristic They form a stout radial skeleton and are developed as a sheath to the radial water vessel Similar ambulacralia are found in the primitive Ophiuroidea

The interambulacral areas are interpreted as collecting organs for small food which, by centrifugal currents, was carried to tube feet placed in basins on the ambulacralia There the small food was picked out from the currents and transported, partially by ciliary action and partially by the tube feet, to the receiving organ placed in the centre of the body This receiving organ is placed within a frame of ossicles, the mouth frame Radially the frame has five deep V's formed from divergent ambulacralia The open angle of the V is continuous with the central opening I am calling the spaces in the angles of the V's 'buccal slits', and interpreting the central opening, continuous with the slits, as a stomodaeum The disposition of the tube feet within the frame can be inferred from the position of their basins These

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* For definition see Glossary, p 124

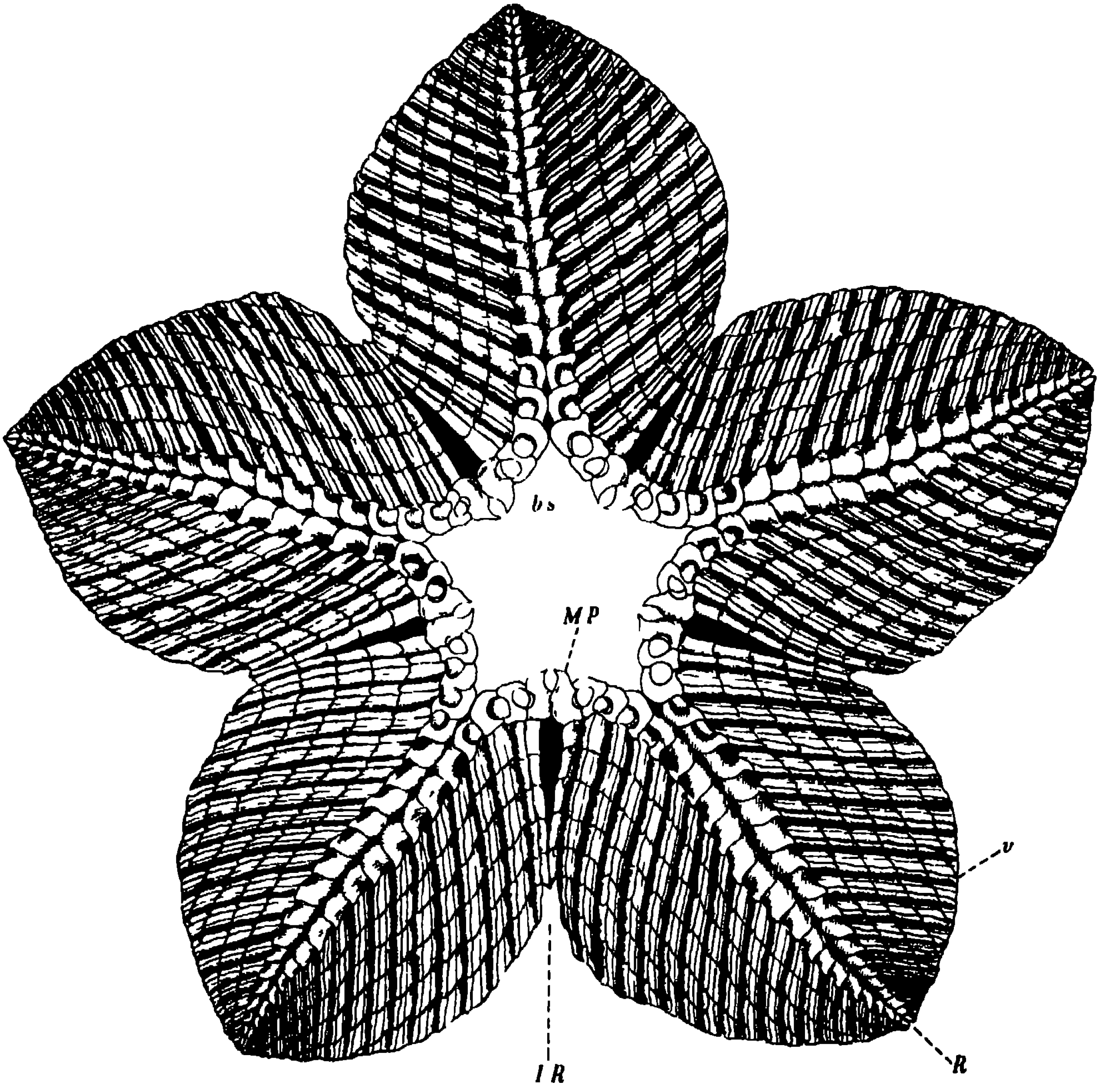


FIGURE 1 *Villebrunaster thorali* n g n sp Reconstruction of the oral surface based mainly on the specimen photographed on the left of figure 29, plate 2 *b s*, buccal slits, *I R*, interradius, *R*, radius, *M P*, mouth-angle plate, *v*, virgalia The double row of ossicles along the radius are the ambulacralia with basins for the tube feet along their outer edges Near the central opening the ambulacralia diverge to form V's of the mouth frame The spaces between the ambulacralia are filled in by rod-shaped interambulacralia (virgalia) The mouth-angle plates are in the interradii and adjoin the central opening

suggest that the food was finally sorted by tube feet alined alongside the slits before entry into the slits and the farther passage to the stomodaeum (p 97)

In all these starfish the interambulacral skeleton, except for the marginal frame of *Archegonaster*, is slightly built Such a skeleton offers slight resistance to the very considerable changes in body shape which can be observed possibly associated with a burrowing habit (see p 97) At one time the body is strongly compressed, at another the body of the same species is well rounded Such changes are brought about in recent animals by well-developed longitudinal and circular muscles which bring about alternate thickening and narrowing of the body

A well-known example is that of the earthworm

Von Uexkull (1921, p 96) has pointed out that such movements provide a pressure which hardens the walls of the burrow and allows free passage of respiratory gases *Sipunculus* employs the same method, whilst the heart urchin hardens the wall by pressure from suitably placed spines All these animals add to the strength of the walls by some form of secretion, in the heart urchin it is mucus

Mucus is a common secretion in Echinodermata and may well have been employed by these primitive starfish Unfortunately, we have no confirmatory information upon the method employed in burrowing by those recent Ophiuroidea which adopt this mode of life We also lack information upon the same habit of the Dendrochirote holothuroids, *Cucumaria* and *Thyone* Hunt (1925, p 570) stated 'Both the above are burrowing forms When feeding, the anterior end of the animal protudes from the burrow and the crown of tentacles is widely extended ' It is difficult to understand the anal respiration of these animals unless 'new' water can freely circulate within the burrow The anus is placed within the burrow

This interrelation of the change of body form form and burrowing habit is also discussed in reference to the structure of the disk of the primitive Ophiuroidea (see p 109)

Order GONIACTINIDA n ord

I am placing all the forms in one order Goniactinida nov with the same characters as those of the subclass

The following families can be recognized

Family Chinianasteridae nov , with the interambulacral skeleton occupying the whole of the interradii

Family Archegonasteridae nov , interambulacral skeleton confined to the outer angles of a pentagonal frame

Family Archophiactinidae Spencer, with no interambulacral skeleton

The progressive loss of skeleton in the history of the subclass may be due to the interference of the skeleton with the muscular activities associated with 'burrowing'

Family CHINIANASTERIDAE n fam

There are two genera, *Chinianaster* Thoral and *Villebrunaster* n g

Villebrunaster n g

Synonymy

Chinianaster pars Thoral, 1935, p 127, plate x, figure 4

Diagnosis

A chinianasterid with small ambulacral basins which served for the insertion of the bases of the tube feet arranged, except near the mouth, along the sides of a tube which is closed along the mid-radius

Type species

V thorali n nom for *Chinianaster levyi* Thoral pars 1935, plate x, figure 4, found in the Upper Tremadoc or basal Arenig in the neighbourhood of St Chinian, Dept Hérault, south France

Material

The fossil was found as impressions preserved in two nodules The larger nodule was split into several fragments which apparently show five specimens in close association The second nodule, only half of an original nodule, shows the oral surface of another specimen

One portion of the larger nodule shows two specimens lying side by side Casts of these are photographed (figure 29, plate 2) The specimen on the left shows the body compressed in a vertical plane, with all the interambulacral areas in the horizontal plane In the second, the specimen on the right, the body is elongated in the vertical plane, and the interambulacral areas are placed at a steep angle to the horizontal plane These different appearances are interpreted in terms of the condition of the body musculature at the time of internment The first specimen had these muscles relaxed and the second had the muscles in a condition of tension It is possible that the latter shows the customary shape of the body The interambulacral areas are in position to face the food in the surrounding sea water, possibly a descending planktonic shower

The specimen with relaxed musculature affords the greater detail and is chosen as the holotype, the remaining material as paratypes All these are preserved in the Villebrun collection of the University of Montpellier, France

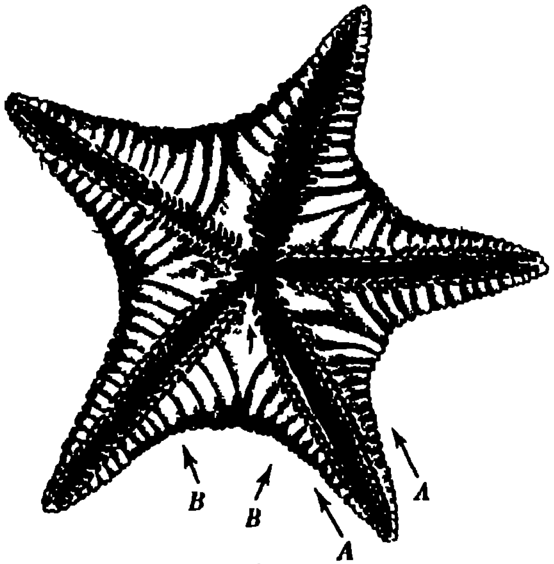
Description of holotype

The oral surface possesses three kinds of ossicles (1) half-cylinders—the ambulacralia—placed along the radii, (2) virgalia often carrying a small keel, the skeleton of the interambulacral areas, (3) mouth-angle plates, a pair of plates placed at each of the interradial angles and projecting into the central opening The groove, characteristic of the typical Asteroidea, is absent as also are adambulacralia (see p 89)

The half-cylinders are stoutly built ossicles which project strongly from the general level of the oral plane (figure 4) They are arranged alternately to enclose a cylindrical hollow which housed the radial water vessel Ambulacralia with these same characters are found in the primitive Ophiuroidea (see p 109) Their surface is excavated into small basin-like hollows which served for the insertion of the bases of tube feet At the extremity of the arm the excavations are placed towards the upper (aboral) edge of the half-cylinders, but they gradually approach the oral plane as the radius is followed towards the mouth The exact structure of the basins is given below in the description of the nearly related genus *Chinianaster*, where they are larger and more fully exposed

The ambulacralia near the mouth form a frame around the central opening The frame is not circular but is prolonged into V's along each radius The broadened end of the V's open into the cavity of the frame The interradial angles are joined together by a pair of mouth-angle plates, short, broad ossicles, almost spade-like in outline

The virgalia are in line and form continuous walls between which are shallow channels The channels run in curved paths from the outer edge of the starfish towards the middle of the arm The floor of the channels seems to have been devoid of calcifications Small areas in the interradial angles (shaded dark in the figures) are also devoid of skeleton



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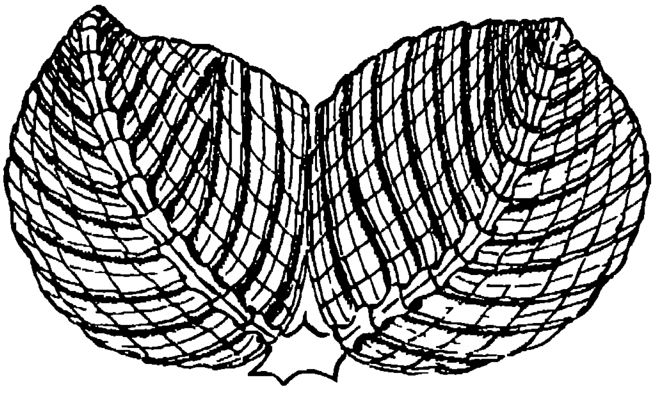

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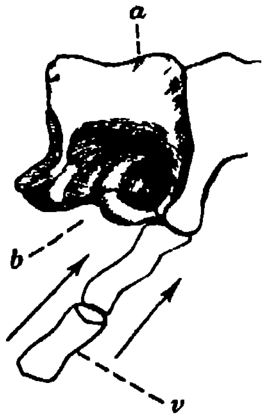

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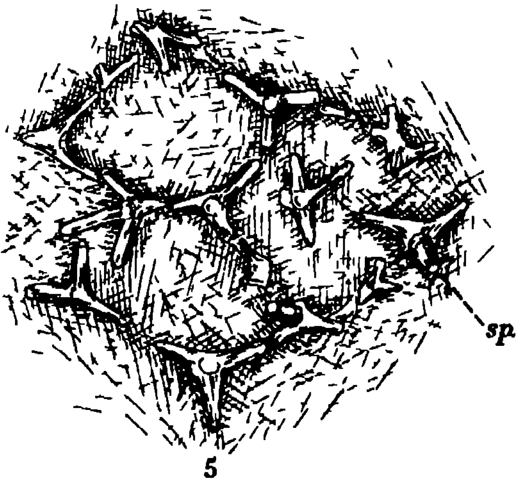

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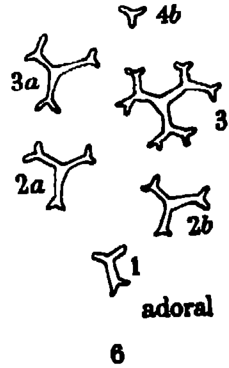

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Figure 2 Oral surface of *Porania* reproduced from Gemmill (1915, plate 1, figure 1) The arrows indicate the direction of the currents *A*, radial currents, *B*, interradial currents

Figure 3 *Villebrunaster thorali* n g et n sp Profile view with body flexed The food-collecting areas face upwards Based on the specimen photographed to the right in figure 29, plate 2

Figure 4 *Villebrunaster thorali* Lateral view of the high ambulacralia with adjoining virgalia, *a*, ambulacralia, *b*, basin for a tube foot, *v*, virgalia The arrows indicate the direction of the incoming current

Figure 5 *Sturzaster marstoni* (Salter) Ossicle of network of aboral surface reproduced from Spencer (1940, text-figure 334) The aboral network of *Chinianaster* is closely similar.

Figure 6 Early stages in the development of the plate of an echinoid, reproduced from Gordon (1926, *B* of figure 1, p 261)

The whole of the aboral surface is covered with triradiate spicules which collectively form a net of wide mesh Impressions of the net are seen in the photographs (figures 30, 31, plate 2) A similar net for *Sturtzaster* is drawn (figure 5)

A collapse of the skeleton after death brought about slight irregularity in the disposition of the mesh It is probable that originally the mesh was regular in pattern with hexagonal interspaces It would then present the same appearance on a macroscopic scale, as is so well shown on a microscopic scale during the development of the echinoderm skeleton (figure 6)

This is a very primitive skeleton which finds some parallel with that of a sponge It forms the background of the aboral skeleton of all later starfish

Interpretation of the structure of Villebrunaster *in relation to function*

The various oral areas are interpreted as follows

(1) Food collecting area—the interradii

(2) Food carriage area—the ambulacralia

(3) Food reception area—the space between the V's of the mouth frame interpreted as buccal slits

Much of this interpretation is based upon Gemmill's investigation (1915) into ciliary nutrition in the Asteroidea Gemmill, when investigating the development of the recent starfish *Asterias rubens*, 'was struck by the constancy and functional importance of the ciliation on the various surfaces (epidermal, endodermal and enterocoelic) of the larva' As the larval ciliation was continued at metamorphosis into that of the adult he made extensive investigation into the role played by ciliary activity in the adult life

Several species of starfish were kept in tanks and deprived of solid food The only food they could obtain was from a continuous current of sea water which had to pass through a hair cloth of fine mesh Under these conditions the starfish *Porania* had not lost any weight after a period of 4½ months, the period from the end of February to the middle of July, during which microscopic material was most abundant in the tanks

Gemmill (1915, p 11) notes several structural or functional peculiarities of *Porania* which, taken as a complex, seemed direct adaptations for ciliary nutrition (figure 2)

(1) The cilia all over the oral surface (in ambulacral grooves, around bases of spines bordering these grooves, on the oral interradii, on buccal membrane, and on denticles) act in such a way that streams of particles are continually converging on the mouth opening

(2) The general shape of the starfish with its large interradial areas ensures that there is an extensive circumoral ciliated field, adapted for food-gathering purposes

Food collecting in Villebrunaster

Villebrunaster has similar large interradial areas which would ensure an extensive circumoral ciliated field The shallow channels between the virgalia follow a precisely similar course to those mapped for the ciliary currents of *Porania* (see Gemmill's diagram)

These currents can be described as adradial They lie at an angle to the radial currents which flow over the surface of the ambulacralia directly towards the mouth

Food sorting and food carriage

All animals which collect food by ciliary fields bring together, at the outset, both nutritive particles and debris In a large number of cases the sorting of these two components is brought about by 'physical' methods Such methods could have been used by *Villebrunaster*, but it seems probable that more use was made of the discriminatory powers of the tube feet

A first 'physical' sorting would be brought about by the loss of velocity when the adradial currents from opposite side meet, change their direction through an angle, and then flow towards the mouth There would be a further loss of velocity because the adradial currents impinge upon the steep walls of the ambulacralia (figure 4) Because of the loss of velocity the heavier debris falls to a lower level This debris would be conducted along the base of the ambulacral walls to find an outlet at the interradial angles already noted as being devoid of skeleton Gemmill (1915, p 3) has noted that there are outgoing currents in *Porania* within these angles (see unlettered arrow in figure 2)

A further and more effective sorting would take place during the radial passage of the food by the use of the discriminatory powers of the tube feet All tube feet have a well-developed sensory system which is associated with the motor nerve supply of the muscles of the tube feet (see, for example, Smith 1937) The reaction of the tube feet to the presence of food has been described by several observers

I have quoted in full (Appendix p 124) the observations of Gislén upon the feeding of *Antedon* These show that the tube feet not only notice the presence of food but take action to throw it into the ciliary produced stream which is flowing towards the mouth Von Uexkull (Appendix, p 126) quotes observations which show that the tube feet of *Ophiothrix* can take similar action, and observes that the food is passed from tube foot to tube foot along a zigzag path, a natural path for a starfish with alternating ambulacralia Gislén also discusses the possible narcotic effects of secretions from glands along this path Such a possibility has also been suggested by Blegvad (Appendix, p 125) as an aid to the opening of a bivalve during the feeding of the Asteroidea

Food reception

The structure of the ambulacralia bordering the buccal slits suggests that the slits were the food-reception areas The basins upon the ambulacralia are lifted into the oral plane, and the tube feet attached to these basins are in position to throw the food into the floor of the slits, whence it would pass to the central body opening It is possible that here was a final selection of food material Observations upon the evolution of the Ophiuroidea (see p 110) show a differentiation of the proximal tube feet, perhaps for this same purpose

The significance of change of the body shape

The second body shape is that photographed in figure 29, plate 2, and drawn in figure 3

The body is elongate in the vertical plane, with its food-collecting areas thrust upwards This body shape is in accordance with its presumed mode of ciliary feeding

The body if compressed in the vertical plane would have its food-collecting surface facing downwards In this position the ciliary channels would tend to choke This would be the more likely if, as seems possible, the starfish lived partially under the bottom mud. The thrust upwards presented the collecting areas to a medium as free from debris as possible A parallel amongst recent echinoderms is given by *Cucumaria*, which Hunt (1925) describes as living buried in the mud with its food-collecting surface (the buccal tentacles) projecting into the clear water above the bottom

Chinianaster Thoral

Synonymy

Chinianaster pars Thoral, 1935, p 127, plate ix, figures 1*a*, 1*b*, plate viii, figure 1, *non* plate x, figure 4

Diagnosis

A chinanasterid with large ambulacral basins placed on the oral surface and separated by a mid-radial open channel

Type species (by original designation)

Chinianaster levyi Thoral

Material

Four specimens, the first, the original of Thoral, 1935, plate ix, figure 1*a*, 1*b*, is here chosen as the lectotype, it was found by Villebrun and is either of Tremadoc or Lower Arenig age, the second, the original of Thoral, plate viii, figure 1, was found by Thoral and is of Upper Tremadoc age, the remaining two specimens were collected subsequent to 1935 by Thoral All came from the neighbourhood of St Chinian, Dept Hérault, south France

Description of the lectotype (figure 7 and figures 35, 36, plate 3)

Oral surface A few of the ambulacralia at the arm extremity are similar to those of *Villebrunaster* There the ossicles are small and narrow, the basins for the tube feet face outwards and the channel between the ambulacralia almost enclosed Proximal to these there is a considerable stretch of arm with broad ambulacralia which have a deep channel running along the midradius, open on its oral surface

This channel, the ambulacral channel (Spencer 1914), is found in the later related genus *Archegonaster* and in all Asteroidea

The basins for the tube feet in this portion of the arm are large and placed almost in the oral plane The build of these basins appears to be primitive since it is similar in all Somasteroidea, palaeozoic Asteroidea and primitive Ophiuroidea The hollow of the basins indicates a rounded seating of the tube feet (possibly an external ampulla, see p 103) The floor of the basin is elongate in the direction of the arm and is shared unequally by two ambulacralia The narrower portion of the floor is on the hinder part of the proximal ossicle, and here the edge of the basin rises steeply The distal portion of the basin is large and the edge gently sloping The branch which leaves the radial water vessel to proceed to the tube feet passes in a gap placed on the proximal inner edge of the basin It thus appears that the tube foot, although seated on the distal portion of a basin, really belongs in origin to the more proximal of the pair of ambulacralia This feature is of importance when considering the evolution of the ophiuroid vertebrae (see p 118)

There are three ambulacralia on each side of a buccal slit The basins within the slits are slightly tilted inwards, but there is no tilt forwards such as is noticeable in *Archegonaster* and the Ophiuroidea The general arrangement of the basins for the tube feet finds a close parallel amongst the Asteroidea found in the early Palaeozoic

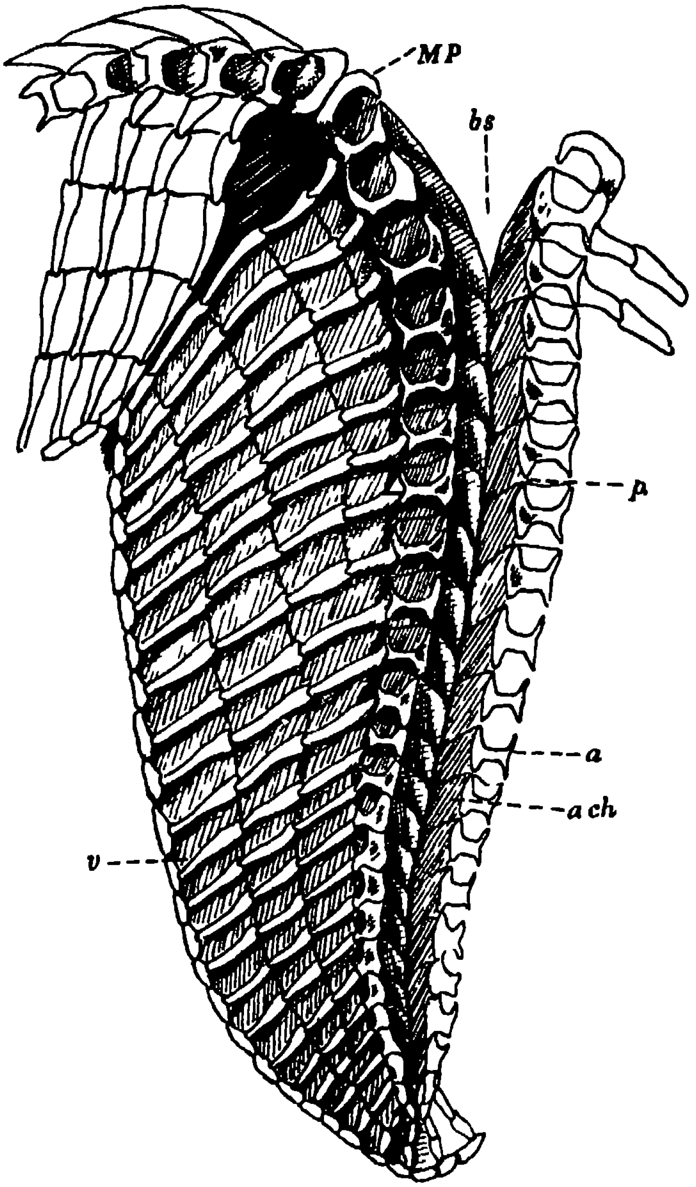


FIGURE 7 *Chinianaster levyi* Thoral Reconstruction of one arm *a*, ambulacral, *a ch*, ambulacral channel, *b s*, buccal slit, *M P*, mouth-angle plate, *v*, virgalia The interradial area, behind the mouth-angle plates, without skeleton is deeply shaded (see p 97)

The structure of the interradial areas is much as in *Villebrunaster*, except that the outline of the margin is not so distinctively petaloid The ossicles at the edge of the disk are closely set, apparently to add to the strength of these edges

A madreporite is present in one of the oral interradial angles It is difficult to decide whether this was its original position or whether it has fallen from a more aboral position *Aboral surface* (figure 36, plate 3) The skeleton extends only over the centre of the body and the arm bases The greater part of the arm appears to be without skeleton

There seems to be little doubt that the central area was considerably swollen, the majority of the ossicles here have collapsed into a heap At the outer edges of the heap there are areas where the typical net appears to be undisturbed The same net can be seen from the oral side within the cavity of the central opening (see the photographs reproduced in figures 35 and 36)

The restriction of the skeleton allows good views of the aboral surfaces of the majority of the ambulacralia They are slightly tumid, closely touching, without any sign of joints or of interskeletal musculature

Description of the remaining syntype and the two small specimens

In these specimens the mouth frame apparently is much enlarged Each V has at least seven ambulacralia, and the ambulacralia which touch one another along the midradii are much reduced in number (figure 8 and figures 32, 33, plate 2)

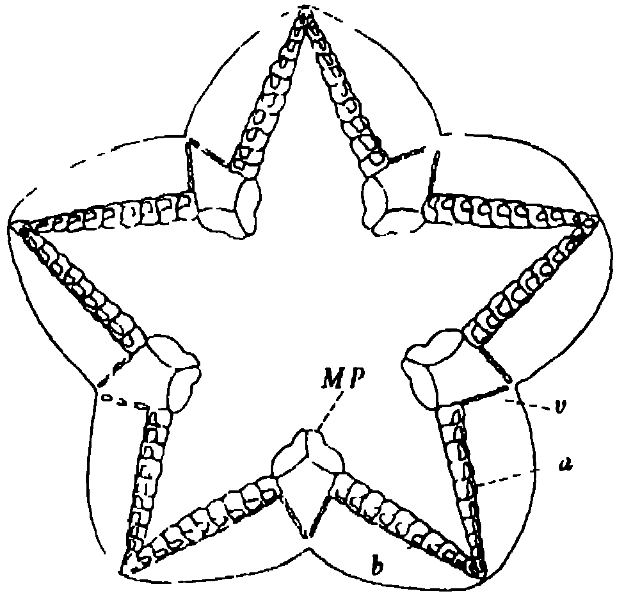


Figure 8 *Chinianaster levyi* Thoral A reconstruction of the mouth frame as seen in a small specimen *a*, ambulacral, *b*, basin for tube foot, *M P*, mouth-angle plate, *v*, virgalia

The explanation appears to be that the V's have become enlarged by a split along the midradial line due to a relaxation (possibly post-mortem) of the musculature which normally held them together The ambulacralia within the V's have in consequence assumed an abnormal tilt which makes their basins slope outwards and not in position to facilitate the handing by tube feet of food into the mouth The musculature which could bring the basins into a feeding position, that is, with their basins tilted inwards, is a ventral cross-musculature which on tightening would bring the inner edges of the ambulacralia nearer to the middle of a radius and at the same time swing their outer edges into the oral place A similar musculature is found in the Asteroidea

Mode of life

The specimens give little information as to the mode of life The basins for large tube feet placed in the oral plane find a parallel in *Archegonaster*

Family ARCHEGONASTERIDAE n fam

Diagnosis

Somasteroidea with bodies bounded by a stout marginal frame, approximately pentagonal in outline, rows of virgalia confined to wedge-shaped area within the outer angles of the pentagon, proximal tube feet were buccal tentacles Adambulacralia present

Remarks

The family contains one genus, *Archegonaster* Jaekel This is found in the $D\gamma_1$ (Upper Arenig) of Bohemia

The relationship of this genus to the early French starfish is shown by the presence of rows of virgalia These, however, do not occupy the whole of the interambulacralia but are confined to limited outer areas It is suggested that they no longer serve as the main organ in nutrition but are retained as an aid in respiration

The orientation of the proximal tube feet suggests that the main method of feeding was by pushing selected bottom material into the mouth by means of the tube feet This method appears to be similar to that adopted in the Ophiuroidea from the time of their appearance and onwards (see p 110)

Both the marginalia and adambulacralia arise as a differentiation of the inner and outer members of rows of virgalia The marginalia are very similar indeed to those found in *Petraster* Billings [*Uranaster* Gregory], the earliest known asteroid, which appears in the Lower Arenig The adambulacralia are cover-plates like those of the Ophiuroidea and quite unlike the adambulacralia of Asteroidea

It is difficult to recognize with certainty any skeletal elements on the aboral surface, except the madreporite

Archegonaster Jaekel emend n

Synonymy

Archegonaster Jaekel, 1923, p 344

Diagnosis

As for family

Type species

I adopt Jaekel's unpublished MS name for the only known species, *A pentagonus* n sp

Material

A considerable number of specimens have been collected from the Upper Arenig $D\gamma_1$ beds of Osek, Bohemia, and are now preserved in the Narodni Museum, Prague The specimen illustrated here in figures 39 and 40, plate 4, is chosen as the holotype Jaekel (1923) gave a very short description His manuscript notes, however, are very full, but my account differs in interpretation largely because I have the earlier French material (unknown to Jaekel) for comparison The abundant material not only allows study of the skeletal units, but the changes in the disposition of the units during the muscle contractions which brought about important arm flexures

The general characters of the form are shown in figure 9

Description

The ambulacralia are built on the same general plan as are those of *Chinianaster*, but they are lighter in construction and show a marked approach to those of the early Asteroidea The large hollow which occupies the midradius in *Chinianaster* is replaced in *Archegonaster* by a shallow channel The ambulacralia however are placed alternately as in *Chinianaster* not opposite as in all Asteroidea.

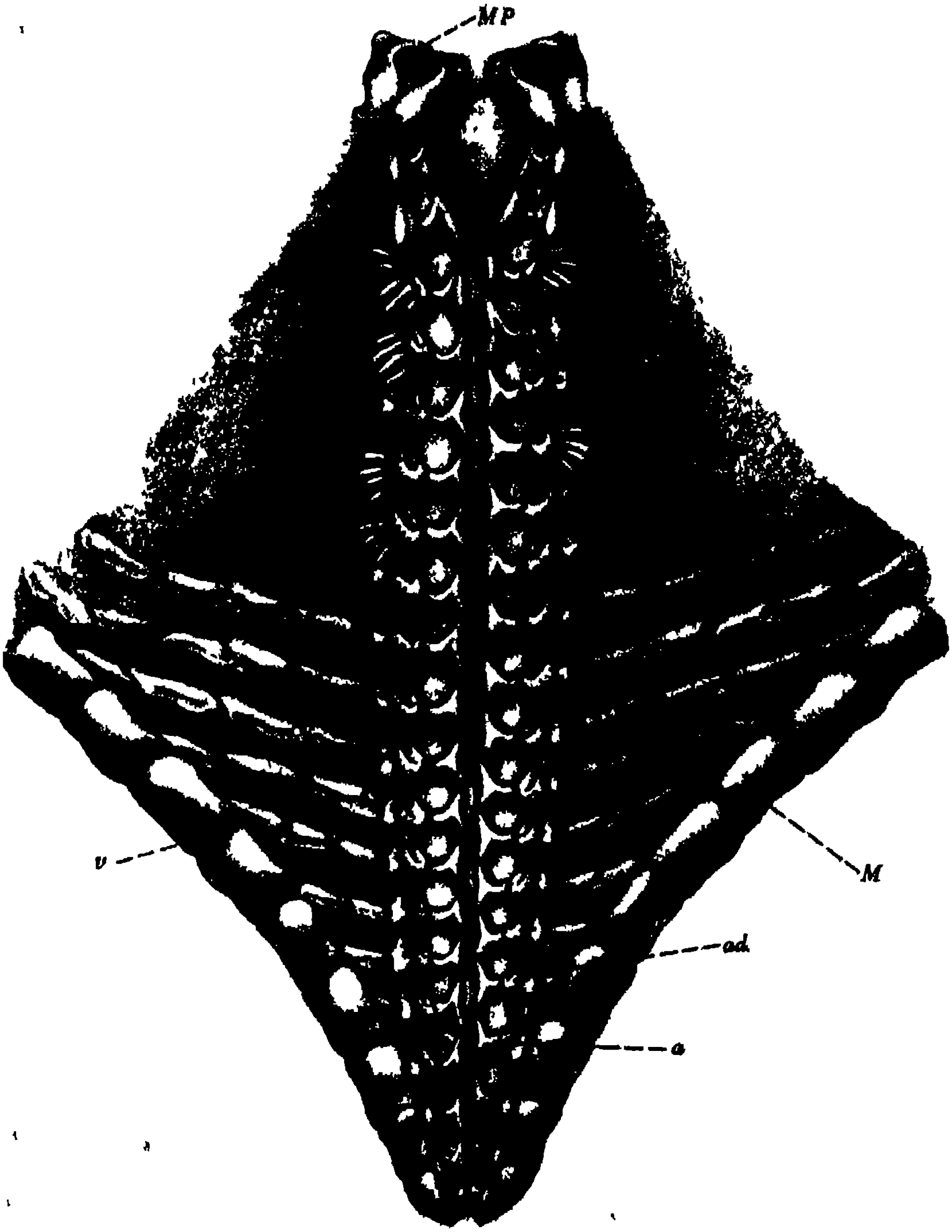


FIGURE 9 *Archegonaster pentagonus* n sp Reconstruction of a portion of the oral surface *a*, ambulacral; *ad*, adambulacral, *b s*, buccal slit, *M*, marginalia; *M P*, mouth-angle plate, *v*, virgalia

The floor of the channel has tongue-shaped projections which overlap proximally (figure 10) Similar tongue-shaped projections have been figured for several Palaeozoic Asteroidea They can be seen in the following genera all figured by Schuchert (1915 *Hudsonaster*, plate 5, figure 1, *Promopalaeaster*, plate 20, figure 2 and plate 23, figure 2, *Urasterella*, plate 27, figure 7 and plate 30, figure 3) I have also figured them for *Schuchertia* (Spencer 1919, p 183) The tongues are important hinges during arm flexion

The basins are large and deep, and it is difficult to see more than their upper edges The tube feet must have been large Jaekel in his manuscript notes makes a suggestion that the deep hollows between the basins were occupied by basal extensions of the tube feet which he called external ampullae, to distinguish them from the internal ampullae of the recent Asteroidea which lie within the body cavity A similar deep basin is seen in the primitive ophiuroid *Eophiura* (figures 19 and 20, pp 114, 115) It is also seen in Palaeozoic Asteroidea No Palaeozoic asteroid shows the pore between the ambulacralia marking the passage to an interior ampulla

A comparison of figures 10 and 11 suggests that the pore area of a recent Asteroid corresponds to the ambulacral basin of these early starfish and that the ampulla has migrated inwards during evolution

The lack of skeleton allows good views of the upper surfaces of the ambulacralia (figure 13) Where they meet along a midradius they look like overlapping tiles Laterally they are prolonged into wings with interspaces If they are compared with a corresponding view of the ambulacralia of the primitive ophiuroid *Palaeura* (figure 26*A*, p 120), many points of resemblance can be noted

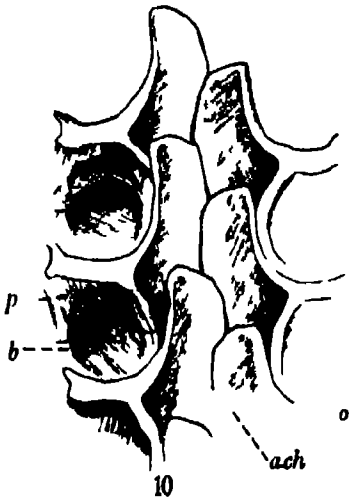
In *Palaeura* there are well-developed midradial balls and sockets and lateral facets for the insertion of longitudinal muscles connecting one ossicle with its neighbour The corresponding structures are seen in *Archegonaster*, but in a more rudimentary stage of development Nevertheless, they functioned to flex the arm dorsally, as in *Palaeura* This was the position of the arm in both forms during feeding

The adambulacralia (figure 12 and figure 54, plate 8) are pear-shaped The broad end of the pear has a thickening upon its oral surface which carried a row of spines These rows are at right angles to the arm axis, and the spines appear to be arranged as a fan The stalk of the pear appears to be short in figure 12, and long in the photograph of figure 54

The apparent increase in length is due to a different placing of the pear relative to the tube feet The extreme end of the stalk is a hinge joint which articulates with the lateral extremity of an ambulacral If the stalk is long the adambulacralia have swung outwards to allow full extrusion of the tube feet If the stalk appears short the adambulacralia have swung inwards to shelter the tube feet The adambulacralia therefore are hinged cover-plates Movement is facilitated by the narrow sutures between successive ossicles

These adambulacralia differ in two important respects from the adambulacralia of the Asteroidea There they are rectangular in outline with broad interossicular sutures Between the sutures are broad muscle bands, the longitudinal adambulacral muscles, which play an important part in maintaining the characteristic asteroid posture (see p 122) In *Archegonaster*, if any longitudinal musculature was present, it was only feebly developed

The second important difference lies in the character of the joint which links the ambulacral with the adambulacral The asteroid adambulacral lies upon a large flat excavation



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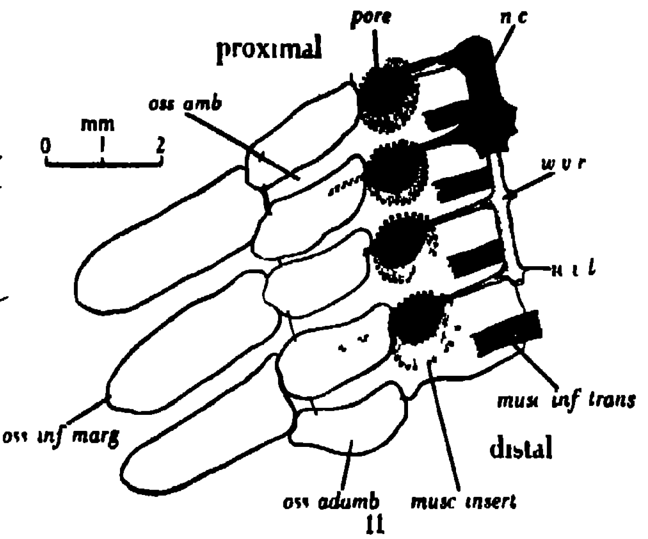

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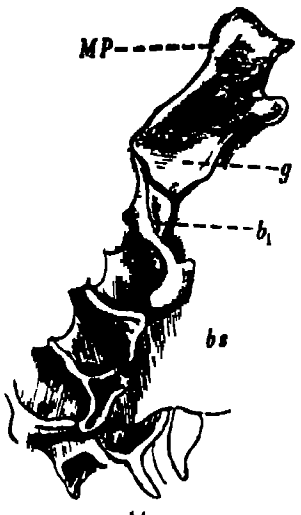

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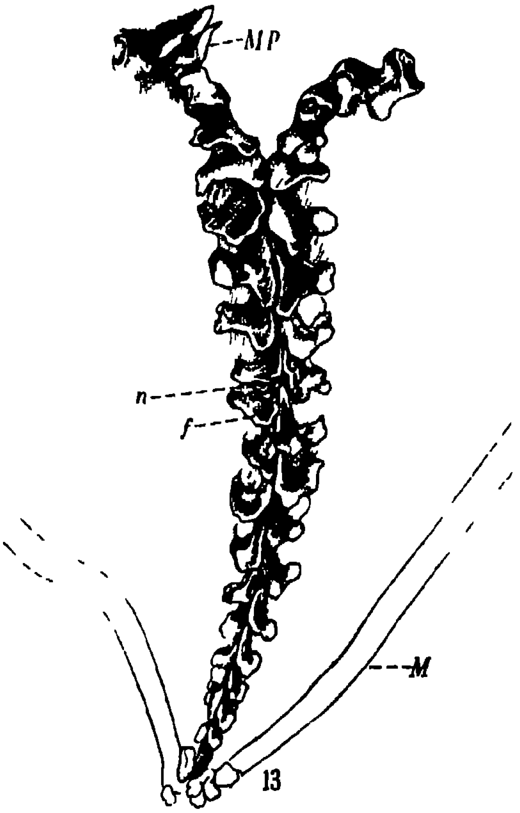

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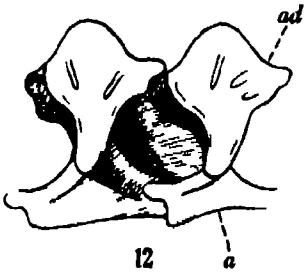

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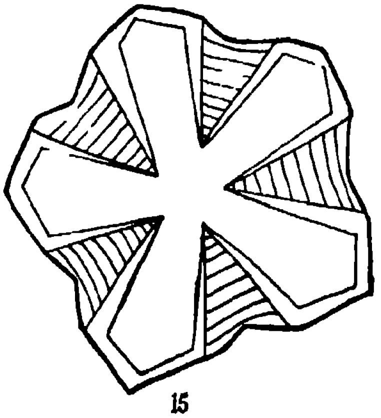

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FIGURE 10 *Archegonaster pentagonus* n sp Ambulacralia enlarged *a ch.*, ambulacral channel, *b*, basin for the tube foot, *p*, passage for branch vessel (from E H 7)

FIGURE 11 Reproduced from Smith (1946, figure 2, p 285) Diagram to show the structures visible on one side of a portion of the ambulacrum of *Astropecten irregularis* after removal of the tube feet and adambulacral and infra-marginal spines Parts of the radial nerve cord and of the radial water vessel have been removed to expose the underlying structures *musc inf trans*, inferior transverse muscle, *musc insert*, insertion of the tube-foot musculature on the ambulacral ossicle,

placed on the oral surface of the ambulacralia (figure 11) The corresponding articular surface in *Archegonaster* is narrow and lateral, a character seen also in the primitive Ophiuroidea (see figure 20, p 115).

As noted above complete rows of virgalia are present only towards the arm extremities The median members of these rows are long narrow plates as in the Chinianasteridae The inner members of the rows, however, are broadened and differentiated as adambulacralia The outer members also have been broadened and differentiated to form portions of the marginal frame The presence of adambulacralia and marginalia in the interambulacral region, otherwise devoid of skeleton, suggests that rows of virgalia occupied the whole of the interambulacral areas in the *Archegonaster* ancestor A loss of skeleton is carried even further in the later representatives of these primitive starfish

The marginalia are thick and triangular in cross-section They are covered with minute granules giving them a roughened surface Between the separate components there are hollows for the insertion of interconnecting muscles or ligaments There is evidence (see below) that the frame acted as an antagonist to the prime-moving muscles during arm flexure

The madreporite opens on the aboral surface It is flat with shallow channels The lack of calcification in the interambulacral areas allows in one specimen (figure 37, plate 3) a good view of its interior face In the centre is a U-shaped furrow for the attachment of the stone canal, resembling a similar furrow in recent Asteroidea Near it is a group of very small ossicles, the scattered small components of the wall of the stone canal

The arrangement of the tube feet within the buccal slits is somewhat different from that in the Chinianasteridae There all the tube feet bordering the slits pointed inwards towards a midradius In *Archegonaster* the more distal tube feet pointed inwards, but the first two tube feet pointed forward, towards the central body opening A view of the proximal ossicles of the slit area is given in figure 14, it is similar to a view of the same ossicles in the primitive ophiuroid *Eophiura* (figure 23), where there is a similar disposition In both cases the mouth-angle plates have a hollow groove which shows the forward angle of protrusion of the podium of the first tube foot The base of the tube foot is housed in a small basin (b_1, figure 14) at right angles to this

It is suggested below (p 118) that the specialization of the proximal tube feet into buccal tentacles is associated with deposit feeding

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n c, radial nerve cord, *oss adamb*, adambulacral ossicle, *oss amb*, ambulacral ossicle, *oss inf marg*, infra-marginal ossicle, *pore*, pore between successive ambulacral ossicles, *w v l*, lateral water vessel, *w v r*, radial water vessel

FIGURE 12 *Archegonaster pentagonus* n sp Ambulacral-adambulacral fitting *a*, ambulacral, *ad*, adambulacral (from E H 11)

FIGURE 13 *Archegonaster pentagonus* n sp Ambulacralia and portion of mouth frame as seen from above, *f*, facets for the insertion of dorsal longitudinal muscle, *n*, nose fitting (incipient ball and socket joint,) *M P*, mouth-angle plate, *M*, outline of marginal frame (from E H 36)

FIGURE 14 *Archegonaster pentagonus* n sp Buccal slit seen from within *b s*, space occupied by buccal slit, b_1, basin for first tube foot, *g*, groove for channel of emergence of first tube foot *M P*, mouth-angle plate (from E H 25)

FIGURE 15 *Archegonaster pentagonus* n sp Diagrammatic drawing showing the arm wedge flexed over the aboral surface (see also figure 34, plate 2)

Arm-flexure feeding and respiration

Specimens which show the animal as a complete pentagon are comparatively rare Most of the specimens show the arm flexed upwards The manner in which this flexure is brought about can be followed from a study of specimens which show stages in the flexure

In the first stage the arc of the marginal frame is drawn sharply inwards and wedges appear in the angles of the pentagon The photograph (figure 38, plate 3) shows the formation of a wedge The frame is drawn inwards towards the central opening It is clear that the pull which brought this about is by musculature placed in the uncalcified portions of the oral surface The marginal frame would be under tension during this muscular contraction and 'by inertia' controls the forces and directs them

In the next stage the wedges are flexed upwards and lie evenly spaced facing upwards (figure 34, plate 2, and figure 15)

The dorsal flexure is possible because of the musculature noted above as inserted on the dorsal surfaces of the ambulacralia The dorsal median ball and socket and the ventral overlap of the oral surface keep the ambulacralia in place during this upward arm swing

This dorsal arm flexure raises the arm wedges, with their rows of virgalia, to face the superficial layers of the bottom mud

The distal tube feet now face upwards, exactly as in the Palaeozoic Ophiuroidea described later Their ability to protrude and reach well out would enable them to search the top layers of the bottom mud, then pull the food downwards into positions where it could be pushed by other tube feet towards the mouth (compare feeding of Atelostomata, p 125)

This reconstruction makes *Archegonaster*, like the primitive Ophiuroidea, a burrowing starfish Animals with such a habit have difficulties with respiration Later it is suggested that the Ophiuroidea meets this difficulty by the provision of respiratory pouches (see p 107) There is no evidence that pouches occur in *Archegonaster* On the other hand, the ciliary currents created within the rows of virgalia placed near the arm extremity would bring along 'new' water This 'new' water passing along the ambulacral channel would enter the mouth and provide for endodermal breathing

Subclass OPHIUROIDEA

Diagnosis

The arms are long and narrow Their musculature is not in the body walls but inserted upon the proximal and distal faces of the ambulacralia where ball and socket joints are developed

The ossicles which border the arm in early forms are hinged (in later forms they are fixed) upon narrow facets on the outer lateral edges of the ambulacralia

The centre of the body is occupied by a 'disk' which has a scale (or granular) skeleton The disk structure is associated with respiratory pouches placed between the oral surface of the disk and the arm

The tube feet act usually as individuals and not collectively

The relationship between structure and function in the primitive Ophiuroidea is discussed below

There is evidence that some of the more important characters of the Ophiuroidea are associated with a 'burrowing' habit Such evidence is provided by (1) the state of the fossil remains, (2) a reconstruction of the mechanisms concerned in respiration

The state of the fossil remains

The body of a starfish readily disintegrates after death and the skeleton is usually scattered If the skeleton is found with its bones in position there were special conditions at the time of death, which favoured preservation A favourable condition would be a 'burrowing' habit, for the starfish died in the grave which it had already dug during its life

The fossil Ophiuroidea described below show not only the whole or considerable portions of their skeleton in place but also indications of the structure and position of the soft parts Decay after death must have been very gradual Mud infiltrated into the hollow of the vessels and hardened The original course of the radial and branch vessels of the water-tube system are well shown in this way, especially in large Ophiuroidea such as *Eophiura* (figure 57, plate 8)

When only portions of the skeleton are preserved they are those which lie deepest in the burrow The majority of the fossil ophiurids, *Pradesura* n g , *Eophiura* Jaekel emend Schuchert and *Palaeura* Jaekel emend Schuchert show only the disk and the arm bases The distal arm regions have been lost Aquarium observations give the reasons for this *Amphiura* is an example After it has burrowed it lives with its arm flexed steeply to the disk The arm extremities project above the sea-bottom and busy themselves with the capture of the rich supply of food available there (Hunt 1925) It is these exposed arm regions which tend to be lost.

The descriptions of the Ophiuroidea given below detail the characteristics of preservation in relation to the presumed burrowing habit

Respiratory mechanisms

The respiratory organs are enclosed gills (respiratory pouches often called 'genital bursae') These pouches are lined with cilia, and their walls project into the cavity of the disk

Two mechanisms are concerned with the change of water within the pouches, (1) ciliary activity and (2) changes in the pressures on the walls of the pouch brought about by pulsations of the walls of the disk

Ciliary activity is the normal method The activities of the disk arise only when the ciliary activity weakens The weakening of ciliary activities has been investigated by Gray (1928) It is brought about when the water immediately surrounding the cilia is impoverished of oxygen and enriched in carbonic acid, that is, under forced respiration

The mechanisms which occur during forced respiration have been described by MacBride (1906, p 485) There are ten radial shields placed on the aboral surface Each articulates with a bar ('genital' bar) Muscles placed on each side of the articulation allow the movement of the shield upon the bar MacBride's observations on *Ophiothrix* show that in this species the articulations allow the radial shields to be raised or lowered

When they are raised, the centre of the disk is lifted into a cone and water is sucked into the pouches, whereas when they are lowered the pouches are compressed and water is expelled He adds in a footnote that he has also observed this in *Ophiura ciliaris* and *Amphiura squamata*

The disk of the early Ophiuroidea has no radial shields or 'genital bars' The upper part of the disk is swollen The scales there fit together loosely whilst at the base they form a firm mosaic skeleton A squeeze of muscles within the body wall would bring about a rise and fall of the upper loosely built skeleton The firm base would not give and the pressure would be exerted on the walls of the pouches arranged around the base

The Palaeozoic genera belonging to the Euzonosomatidae (Spencer, 1930, p 405) have the base of the disk further strengthened by a marginal frame

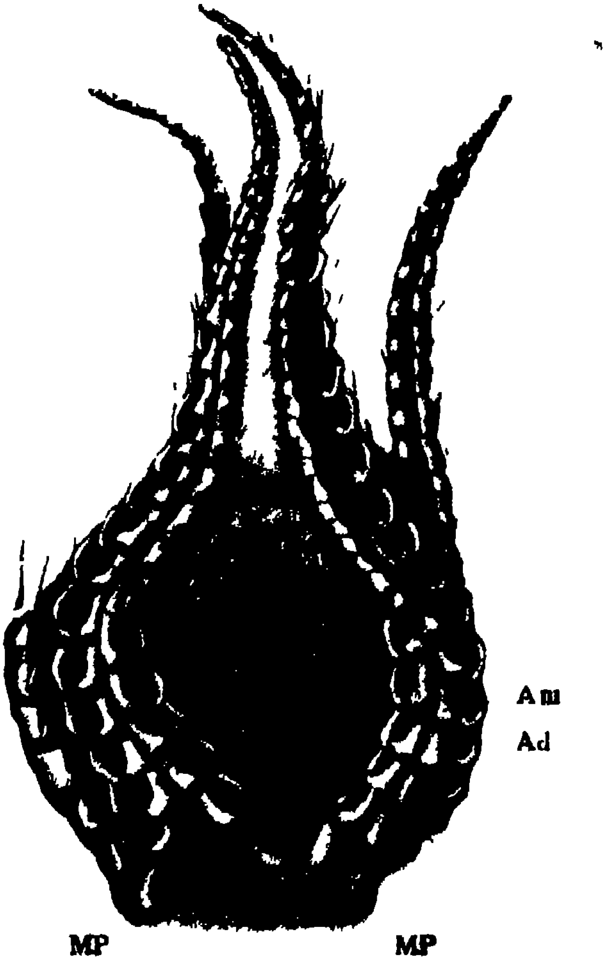


FIGURE 16 *Taeniaster spinosus* (Billings) A small specimen showing the arms flexed steeply over a swollen disk (copied from Spencer 1922, text-figure 140) *Ad*, lateral, *Am*, ambulacral, *M P*, mouth-angle plate

Other activities of the Ophiuroidea within the burrow

I have not seen any observations upon recent burrowing Ophiuroidea which describe the burrow itself or deal with the difficulties of respiration and transport of food associated with the burrowing habit Examination of the fossil material suggests the methods which were employed by the early Palaeozoic forms to meet the problems

The transport of small food to the mouth, placed as it is at the bottom of the burrow, could only be effective if the surrounding sand or mud be excluded from the food channel

A tunnel through the mud is provided by the ossicles (lateralia) at the edge of the arms These carry a border of long spines The lateralia with their spines can swing over and form the walls and roof of such a tunnel A specimen of *Eophiura* (see p 117) shows such a tunnel

It is probable that an ophiuroid can harden the walls of the burrow and thus provide space between the animal and the surrounding mud for free circulation of 'new' water This problem has been considered by von Uexkull (see p 93) In all the cases quoted the animal exerts pressure upon the surrounding medium to form a wall and then cements the particles of the wall by mucus or similar material

In the case of the ophiuroid, pressure to form the wall would arise from alternate narrowing and widening of the disk as described above Such movements would become more active in forced respiration, that is, when a supply of 'new' water was in process of being cut off In this way lack of new water would automatically bring into being new pressures to form the wall

The Ophiuroidea and the primitive echinoderm stock

The ambulacralia

The early Ophiuroidea have characters which suggest that they are near to a primitive echinoderm stock

The ambulacralia are very similar to those of *Villebrunaster*, a starfish which shows the beginnings of skeletal differentiation In both the ossicles are developed within the sheaths enclosing the radial water vessel, and their tubular cross-section shows no sign of any mid-radial groove, which in the Asteroidea houses the broad thick radial nerve cord Smith's investigations show this nerve to possess definite cable-like tracts providing paths for the rapid conduction of impulses from the sensory elements of the ectoderm to the circum-oral nerve ring, the centre responsible for the maintenance of co-ordinated movement of the tube feet and arms

The absence or presence of a well-developed radial nerve cord is linked with the methods of feeding In the Asteroidea (see p 122) feeding is a result of the co-ordination of tube feet and arms

In the Ophiuroidea there is no such co-ordination In an account of the suggested method of feeding of *Villebrunaster* (see p 97) I drew comparisons between the possible method employed by the primitive starfish and the accounts given of the capture of small food by the recent crinoid *Antedon* and by *Ophiothrix* In each form every tube foot acts as an autonomous agent It recognizes a food particle, places itself adjacent and then pushes the particle into the food channel There it is recognized by an adjacent tube foot and pushed farther along Eventually the proximal tube feet push it into the mouth During feeding on small food the arms, both of the Crinoidea and of the Ophiuroidea, act merely as supports of the tube feet during the period in which the tube feet are engaged in food capture and transport In the asteroid both arms and feet work together in the feeding activities to bring the food nearer the mouth

Upon the evidence available it would seem that the condition in the Crinoidea and the Ophiuroidea where the tube feet act as isolated elements is more primitive than that in the Asteroidea which have acquired an equipment of association elements within the sensory system

The aboral skeleton

The scales of the aboral surface of *Pradesura* and some other early Palaeozoic Ophiuroidea (figure 18) have a radiate cap The disposition of the branches of the caps recalls the radiate spicules of *Villebrunaster*, and suggests that the scale has been formed by shallow infillings between the branches Support is given to this view by the structure of the aboral ossicles of *Sturtzaster* This Silurian ophiuroid has a high swollen disk with ossicles which have reverted to the *Villebrunaster* type (figure 5, p 95)

The mouth frame

The mouth frame in the Arenig Ophiuroidea has deep radial V's, a character also found in the Somasteroidea (see p 92) and in the early Asteroidea (see p 123) The interpretation suggested is that the V's represent the marginal skeleton of buccal slits which in the common echinoderm ancestor opened into a central stomodaeum

The stone canal

A stone canal is present in recent Asteroidea but not in recent Ophiuroidea It is present in the early Ophiuroidea (see p 116) and in the Somasteroidea (see p 105)

The buccal tentacles

A characteristic of recent Ophiuroidea is that the first two pairs of tube feet are enlarged and placed in position to reach into the stomach In origin they are the proximal elements of the tube feet placed within the buccal slits where, it was suggested (see p 92), the selection of nutritive from non-nutritive material mainly occurred These buccal tentacles can be regarded as making the final decision upon the material passed into the stomach The orientation of these tube feet is an important factor in the evolution of the ophiuroid 'jaw'

The first stage in the orientation brings the mouth-angle plates into alinement with the first ambulacralia In the early Ophiuroidea only the first pairs of tube feet are buccal tentacles Food selection in this way does not occur in the Asteroidea which never have buccal tentacles

Classification

I am dividing the Ophiuroidea into

Order Stenurida n ord The ambulacralia have not become vertebrae The arm is capable only of limited movements

Order Ophiurida n ord The ambulacralia have become vertebrae The arm is capable of snake-like movements

Order STENURIDA n ord

All the Arenig Ophiuroidea, with the exception of *Hallaster* known from one solitary specimen, belong to this order The genera described here are *Pradesura* n g (Basal Arenig), *Eophiura* Jaekel emend Schuchert and *Palaeura* Jaekel emend Schuchert (Upper Arenig)

All have

(1) Ambulacralia formed in a sheath which enclosed the radial vessels Each tube foot was placed in a basin shared by two ambulacralia

(2) A clearly defined disk with a 'scale' skeleton

(3) A mouth frame with radial V's The ossicles within the V's are fused, and each arm of the V acts as a unit during the opening of the frame

(4) The ossicles bordering the arm (lateralia) are hinged to the ambulacralia and act as covering plates to the groove They correspond in position to the side-shields of the Ophiurida, but these latter are fixed not hinged

The lateralia usually can be recognized as a double series In a previous publication (Spencer 1940) I called the members of the double series outer and inner lateralia Jaekel uses the terms lateralia and sublateralia for these same two series, and his terms prove to be more suitable for the purposes of description

Classification of Stenurida

1 Superfamily Eophiuricae n superfam

Stenurida with the basins for the tube feet placed subequally on two ambulacralia

(*a*) Family Stenasteridae Schuchert 1915 emend n Lateralia broad, each carrying several rows of spines

Stenaster Billings

(*b*) Family Eophiuridae n fam Outer lateralia broad with a single row of spines placed parallel to the arm axis

Eophiura Jaekel emend Schuchert, *Rhopalocoma* Salter, *Ptilonaster* Hall

(*c*) Family Pradesuridae n fam Outer lateralia broad with a single row of spines placed at an angle to the arm axis

Pradesura n g , *Sturtzaster* R Etheridge junr

(*d*) Family Phragmactidae n fam Outer lateralia narrow, spines in single row at right angles to arm axis

Phragmactis Spencer, *Bdellacoma* Salter

2 Superfamily Palaeuricae n superfam Stenurida with the basins for the tube feet placed almost entirely on one ambulacral

Family Palaeuridae n fam *Palaeura* Jaekel emend Schuchert

Pradesura n g

Synonymy

Palaeura Thoral, 1935, p 123 *non* Jaekel, 1903

Diagnosis

A stenurid of the family Pradesuridae with a well-plated disk and spines on the lateralia placed upon a ridge which runs at an angle to the arm's length Ambulacral basins shared subequally by two ambulacralia

Type and early known species

Palaeura jacobi Thoral (1935, p 123, plate ix, figures 2–5) Basal Arenig, Prades sur Vernazobres, near St Chinian, Herault, South France and near localities

Material

The collections of the University of Montpellier contain seven specimens, three with counterparts The central parts of the starfish are well preserved, but none of the specimens shows the distal parts of the arm

Lectotype

The specimen figured by Thoral (1935, plate ix, figure 2 (here figure 41, plate 5))

Remarks

Pradesura is the first ophiuroid to appear

Its nearest relation is *Sturzaster* from the Silurian This has a disk which is very swollen and devoid of scales

The two characters which differentiate the genus from *Palaeura* are (1) the spines on the lateralia, in *Palaeura* parallel to the arm's length, (2) the basins for the tube feet, shared subequally by two ambulacralia in *Pradesura*, almost entirely upon one ossicle in *Palaeura*

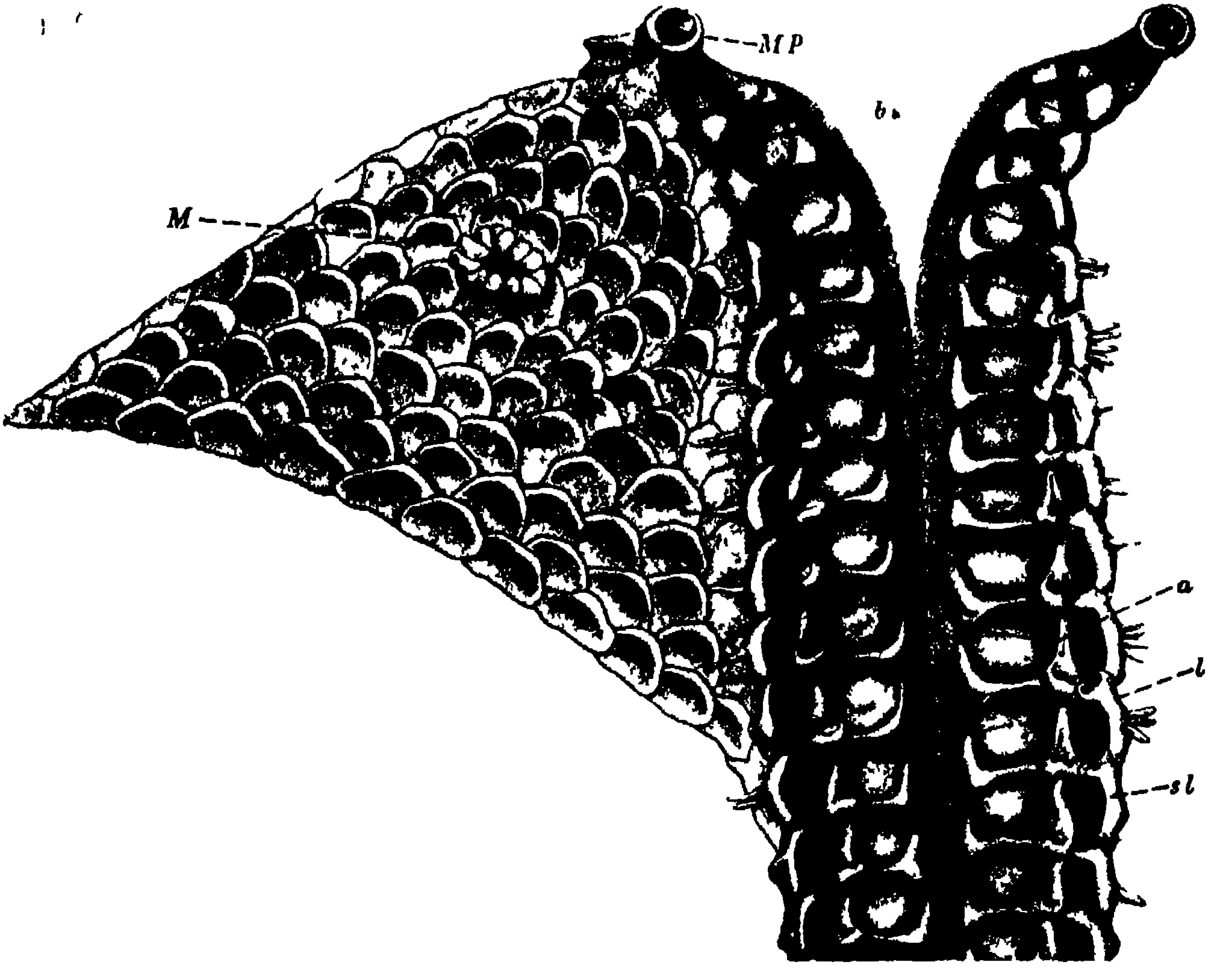


FIGURE 17 *Pradesura jacobi* (Thoral) Oral view of a portion of the disk and the neighbouring arms *a*, ambulacral, *b s*, buccal slit, *l*, lateral, *s l*, sublateral, *M*, madreporite, *M P*, mouth-angle plate

Description

The arms (figure 17) have a thick central core of stoutly built ambulacralia and a narrow edging of lightly built lateralia Although they are typically ophiuroid they have features which link the genus with the Chinianasteridae The ambulacralia, in particular, have marked resemblances to those of *Villebrunaster* They are placed alternately on each side of the arm, and collectively form a thick sheath to the radial water vessel The basins for the tube feet throughout the greater part of the arm are excavated on the lateral margins of the sheath and the floor of each basin is shared by two neighbouring ambulacralia

Some specimens, because of the collapse of the aboral covering of scales, allow views of the ambulacralia from above The best of these views is given by No Px coll Marty 1937, figured here (figure 44, plate 5) It shows ball and socket joints and facets for the insertion of the dorsal longitudinal muscles, similar, but less well developed, to those figured for *Palaeura* (figure 26*A*, p 120)

The proximal ambulacralia form a mouth frame with radial V's similar to that of *Villebrunaster* in the number of ambulacralia (3 × 2) in each V This is a smaller number than those present in the radial V's of *Palaeura* and *Eophiura*

The disposition of the ambulacral basins within the frame follows that described above, p 110 The first tube feet only are 'buccal tentacles' The mouth-angle plates are very similar indeed to those of *Sturzaster* (Spencer 1940, text-fig 337)

Both lateralia and sublateralia are present The lateralia carry a row of spines placed on a slight ridge set almost at right angles to the arm length The ridge passes over the entire width of the slightly swollen oral surface and then on to the lateral surface The spines project outwards from the arm Usually they are not well preserved, and in the specimen drawn (figure 17) they are only represented by their bases

Specimen no 140 shows impressions of long thin spines very similar to those of *Sturtzaster* (Spencer 1940, figure 33, p 519)

The sublateralia, as is usual, carry no spines They are long, narrow and thickened at their distal edge and lie alongside the ambulacralia with their greatest length along the arm radius There are slight displacements here and there which suggest that the lateralia and sublateralia had not fused

They could swing to shelter the tube feet The specimen photographed in figure 43, plate 5, shows the lateralia in such a position

The scales of the disk differ somewhat in form and disposition upon the two surfaces On the oral surface they form a firm skeleton Their rather irregular rows show no trace of association with the ambulacral skeleton noticeable in the Somasteroidea The disk margins are straight or concave, not rounded as is usual in recent Ophiuroidea One specimen (figure 42, plate 5) shows long thin spines on the scales near the margin

On the aboral surface the scales fitted more loosely (figure 44, plate 5) and occasionally they have collapsed in heaps as if they had fallen from a tumid surface Many show the radiate cap described above, p 110 Specimen no 137 shows that each cap carried a long spine similar to that carried by *Taeniaster* (Spencer 1934, text-fig 292)

The madreporite is a small rounded thick ossicle with comparatively few surface channels It is placed slightly to the left of a mid-interradius and near the interradial angle (figure 17)

Eophiura Jaekel, 1903 emend Schuchert, 1915

Synonymy

Eophiura Jaekel, 1903, p 107, *Eophiura* Schuchert, 1915, p 222, *Eophiura* Jaekel, 1923, p 347.

Diagnosis

A stenurid of the family Eophiuridae with a well-plated disk with small overlapping scales, spines set parallel to the arm's length, ambulacral basins shared subequally by two ambulacralia, ambulacral axis broad and stiff, paired mouth-angle plates broadly notched proximally

Type (and only known) species

E bohemica Schuchert, 1915 (= *E petaloides* Jaekel, 1923) from the Upper Arenig, Dγ_1, of Osek, Bohemia

Material

The original specimen illustrated by Jaekel (1903, text-figure 4) is here chosen as the lectotype of *E bohemica* That author gave two figures together with a short description

Both are of the oral surface One figure was drawn from the lectotype and the other from the specimen, here illustrated as figure 56, plate 8 The lectotype, like so many ophiuroids from the Arenig, shows only the disk and the arm bases The second specimen gives an oral view of the distal arm regions flexed over the disk in a position I am interpreting as that adopted for feeding (see p 117) Three other specimens show portions of the middle of the arms flexed steeply to the disk as in figure 57, plate 8

Jaekel made further observations in 1923, but gave only a diagrammatic figure, the basis for my figure 19 His views are further elaborated in his manuscript I have found that I could add little from my own observations, but, at times, I differ somewhat in interpretation

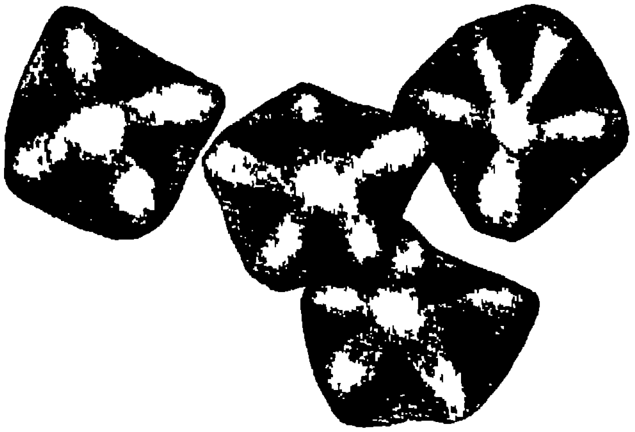


FIGURE 18 *Encrinaster grayae* Spencer Scales from the aboral surface (copied from Spencer 1930, text-figure 260, p 406)

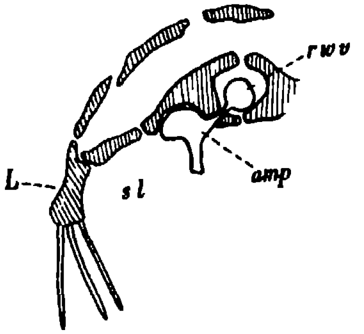


FIGURE 19 *Eophiura bohemica* Schuchert Diagrammatic cross-section of arm, after Jaekel *amp*, external ampulla, *L*, lateralia, *s l*, sublateralia, *r w v*, radial water vessel

Description

The ambulacralia resemble those of *Pradesurae* in that the basins for the tube feet are shared almost equally by two ambulacralia They differ in two characters, the basins are nearer the oral surface, and the hollow between the ambulacralia housed a large radial vessel (figure 57, plate 8)

The basins are deep, and Jaekel in his MS notes suggests that, as in *Archegonaster*, they were occupied by external ampullae Towards the end of the arm (figure 20) they are oval but broaden laterally as they are followed towards the mouth The anterior and posterior edges of the basins show a distinct groove (figure 48, plate 6) which probably was occupied by a lateral branch of the perihaemal canal surrounding the tube feet

There are slight roughenings on the floor of some of the basins which may indicate the positions of attachment of the bases of the tube feet

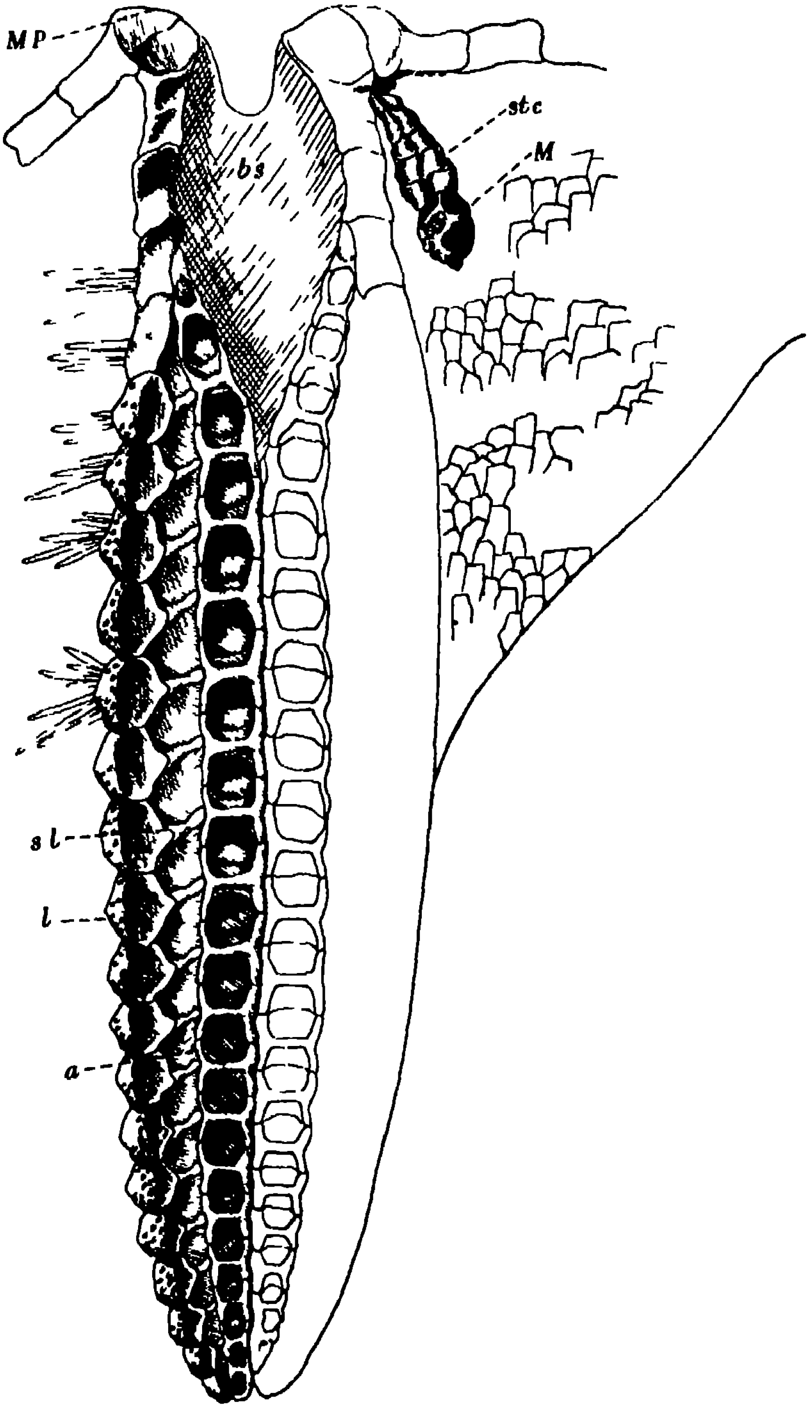


FIGURE 20 *Eophiura bohemica* Schuchert Oral view of the arm and a portion of the disk *a*, ambulacral, *b s*, buccal slit, *l*, lateral, *s l*, sublateral, *M*, madreporite, *M P*, mouth-angle plate, *st c*, stone canal (based on E H 94 and E H 101)

The sides of the basins are thickened along their radial edges to form a series of longitudinal ridges which meet across the middle line These ridges usually hide the large hollow between the opposite ambulacralia Occasionally, however, the ambulacralia have fallen apart exposing the hollow in full depth This is very similar to the hollow in *Chinianaster* Some casts also show a tear where the side branch to a tube foot left the radial vessel This tear is always immediately behind the cross-ridge, the thickened edge which separates two basins (figure 50, plate 7)

The tear always points backwards, and the branch vessel therefore followed the same path as that in a recent asteroid (figure 11, p 104)

At the extreme outer edge of a basin is a small shallow depression which housed the muscle connecting an ambulacral with a sublateral

The ambulacralia are well exposed from above in several specimens They are rectangular in outline and convexly curved, so that they appear almost cylindrical in cross-section They fit closely, but here and there are signs of the former presence of dorsal muscles (figure 22) This drawing shows the ossicles slightly dislocated with an overlap upon a slightly curved fitting The overlap brings the outer upper edge of one ambulacral over its predecessor

Both lateralia and sublateralia are present They articulate by means of well-developed ball and socket joints The effect of this articulation is to impart a wide swing to the movements of the lateralia

The lateralia, when the swing outwards is at a maximum, show large flat surfaces, which, at their extreme outer edges, carry spines placed in a row parallel to the arm length Near the arm extremities this single row is replaced by spines scattered irregularly on the faces of the ossicles (figure 52, plate 7)

The sublateralia are slightly twisted rods Their outer ends are broad, and where they meet the lateralia ball and socket joints are well developed Their inner ends are pointed and rest upon small hollows placed on the outer edges of the ambulacralia

The buccal slits were deep and the proximal ambulacralia bordering them tightly joined together Each arm of the V extends forward to form an alinement with a mouth-angle plate Between a pair of mouth-angle plates there is a proximal deep cut in the ossicles This housed a muscle which could thrust the frame by the V's widely open The mechanism of this movement was dealt with in an earlier communication (Spencer 1925, p 264)

The only distinction between the structure in *Eophiura* and that in the later Ophiuroidea described in that communication is that the V here is made from a number of ambulacralia, whilst in the later Ophiuroidea it is built from the enlarged first pair of ambulacralia only

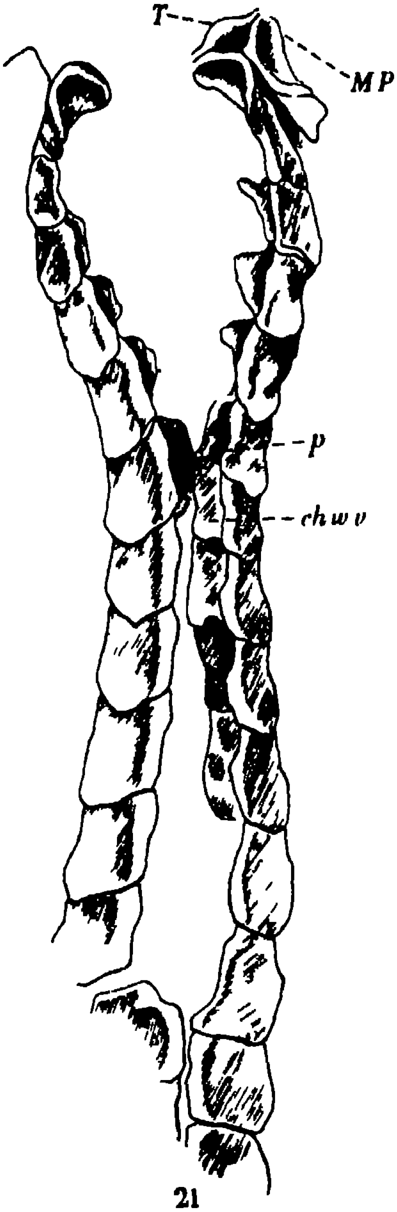
The positions of the basins for the first tube foot are as in *Archegonaster* (see p 105) The first pair of tube feet could project as 'buccal tentacles' into the central opening

In one of the buccal slits of the specimen, E H 94, there is a displaced torus It is a narrow and thin plate and is furnished with a row of long spines set along the length of the plate

The specimens show a well-ossified stone canal (figure 47, plate 6) The greater part of the length of the canal is shown by the specimen in figure 20, p 115 This is the stretch between the madreporite and the lower edge of the mouth frame The part of the canal attached to the central 'ring' is shown in E H 105, where the mouth frame is exposed from above.

Mode of feeding

The state of preservation of the fossils suggests that the animal lay buried in the mud with the more distal parts of the arms flexed upwards and then brought parallel to the upper layers of the sea-bottom (figure 56, plate 8) The mud, rich in detritus, would be scooped by the upwardly projecting tube feet and pushed along the arm to the mouth Specimen E H 100 shows the lateralia swung inwards at the edges of the buccal slits, with their



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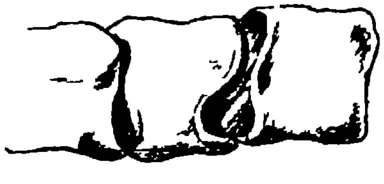

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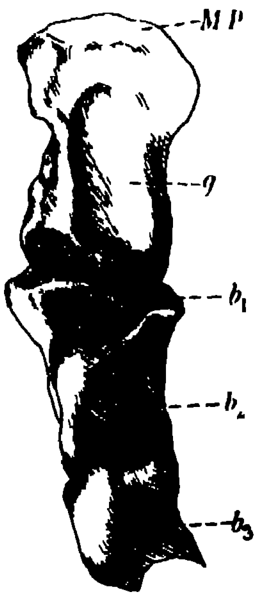

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FIGURE 21 *Eophiura bohemica* Schuchert Mouth frame and ambulacralia seen from above *M P*, mouth-angle plate, *p*, pore for passage of branch water vessel, *ch w v*, channel for radial water vessel, *T* torus (from E H 105)

FIGURE 22 *Eophiura bohemica* Schuchert Aboral surface of slightly displaced ambulacralia showing the articulations between them (from E H 105)

FIGURE 23 *Eophiura bohemica* Schuchert An angle of the mouth frame seen in side view b_1, basin for first tube foot, b_2, basin for second tube foot, b_3, basins for the third tube foot, *g*, groove for first tube foot, *M P*, mouth-angle plate (from E H 105)

spines completely roofing over the ambulacral groove Through the tunnel thus formed the food would be passed to the mouth Some selection of food from debris was probably made by the buccal tentacles

Palaeura Jaekel, 1903, emend Schuchert, 1915

Synonymy

Palaeura Jaekel, 1903, p 110, *Palaeura* Schuchert 1915, p 223

Diagnosis

A stenurid of the family Palaeuridae with a well-plated skeleton and with ambulacral basins seated almost entirely on one ambulacral

Type (and only known) species

P neglecta Schuchert, 1915 From the Upper Arenig, Dγ_1 of Osek, Bohemia

Material

There are many specimens The majority, like those of *Pradesura*, show only the disk and the arm bases, that is, the arm extremities were washed away before preservation Five specimens, however, show one or more complete arms These are always found with their arms bent backwards over the disk with their oral surface uppermost (figure 60, plate 8) This is a position comparable to that found in *Eophiura* (figure 56, plate 8) The tube feet are in position to feed from the superficial layers of the sea-bottom A further specimen shows a profile view which can be compared to that shown by the lower half of the specimen drawn in figure 16, p 108) It is photographed in figure 59, plate 8 The disk is tumid and the bases of the arms are flexed to wrap around it A comparable view is presented by a specimen of *Eophiura* (figure 57, plate 8)

Remarks

A short description of this genus with a very diagrammatic text-figure was given by Jaekel in 1903 The MS notes of Jaekel are almost entirely devoid of further description

Palaeura has a considerable general resemblance to *Pradesura* The special features of interest are

(1) The state of preservation of the material This supports the views already advanced of the mode of life of these primitive Ophiuroidea

(2) The ambulacral basins which show a marked advance towards the basins prevalent in the Ophiurida, that is Ophiuroidea which have their ambulacralia constructed as 'vertebrae'

Description

Palaeura is the earliest known ophiuroid to show the marked change in the seating of the tube feet which accompanies the completion of the formation of 'vertebrae' In all the starfish described in the previous pages the floor of each ambulacral basin was shared subequally by two ambulacralia, the larger portion of the seating being upon the distal member of the pair In *Palaeura* (figure 24) the basin is still shared by two ambulacralia, but by far the larger portion of its floor is upon the proximal member of the pair Only a very small portion of the basin is on the distal ambulacral

This change in seating has taken place by an elongation of one ossicle which has captured the seating from its more distal neighbour Ludwig (1881) many years ago pointed out that such a capture must have taken place during evolution He arrived at this conclusion after observations on the early developmental stages of the ophiuroid vertebra The 'anlage' of a vertebra is a triradiate spicule with a definite orientation The branches of the spicule are subequal each with a definite orientation Two are directed adoralwards, one along the length of the arm, the other at an angle to it (figure 27*C*) The third branch, also along the length of the arm, is directed aboralwards In the next stage the spicule is still triradiate, but the aboral branch has elongated (figure 27*D*) These proportions are retained during the further growth of the vertebra

Ludwig compared this growth of the ophiuroid spicule with an imaginary Asteroid 'anlage', and came to the conclusion that the tube feet in the ophiuroid moved forward relatively to the ambulacralia The tube foot, e g of the twelfth vertebra of an ophiuroid, corresponded to the tube foot placed between the twelfth and thirteenth ambulacral of an asteroid

The comparable evidence afforded by embryology and palaeontology can be best illustrated from figures which show the strong ridges marking the boundaries of the basin in which the tube foot is seated These ridges have the same form as the spicular 'anlage' Figure 27*A* shows them in *Eophiura*, where the basin is shared subequally by two ambulacralia The disposition of the ridges is exactly as in the first stage in the ophiuroid development, all the branches being subequal The next stage is shown by *Palaeura* (figure 27*B*), where the aboral branch has elongated

The new growth takes place immediately behind the branch vessel to the tube foot Several specimens of *Palaeura* are preserved with this branch filled in with hardened mud, and the casts show that the vessel entered the basin just behind the cross-ridge which separated the basins from each other (*p* of figures 27*A* and *B*) This is the same position as in both *Eophiura* (figure 50, plate 7) and the Asteroidea (figure 11, p 104) The position of the branch vessel has not altered, and the new growths are confined to the regions behind the vessel In later evolution the branch vessel itself must have been caught up in the new growth Otherwise it is difficult to explain the tortuous course of this vessel (see, for example, Ludwig 1878)

Order OPHIURIDA n ord

Diagnosis

Ophiuroidea with ambulacralia changed into vertebrae

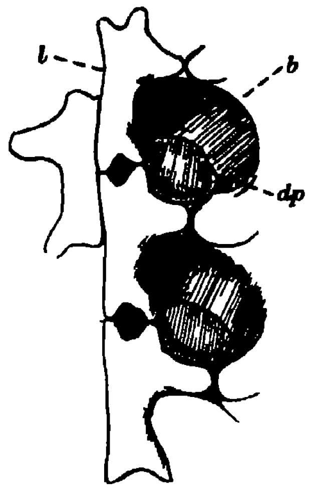
A drawing (figure 25) from a mid-Ordovician ophiurid (*Taeniaster*) shows the completion of the 'vertebral' structure The basin is on one ambulacral, and there are pits for the insertion of the two ventral muscles

Suborder OEGOPHIURINA (subclass Oegophiuroida Matsumoto)

Diagnosis

Ophiurida with an open ambulacral groove

Superfamily Lysophiuricae (order Lysophiurae Gregory) with ambulacralia alternating contains families Protasteridae Spencer, Euzonosomatidae Spencer and Cheiropterasteridae Spencer



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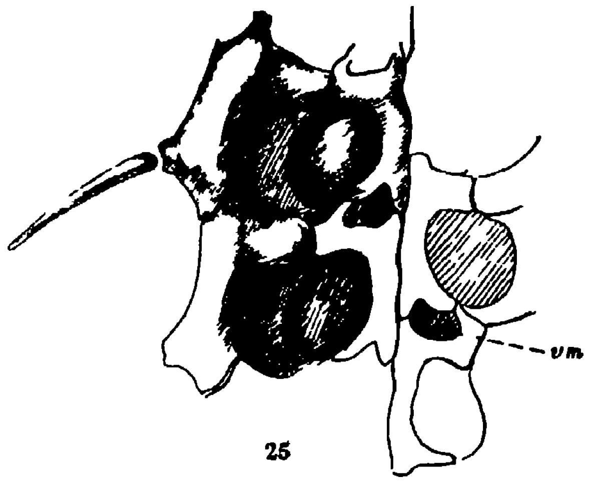

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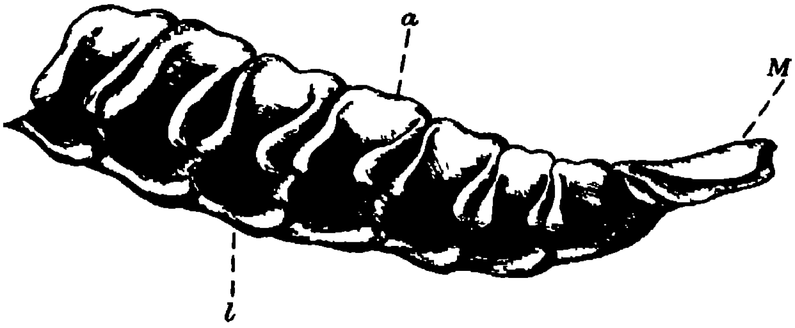

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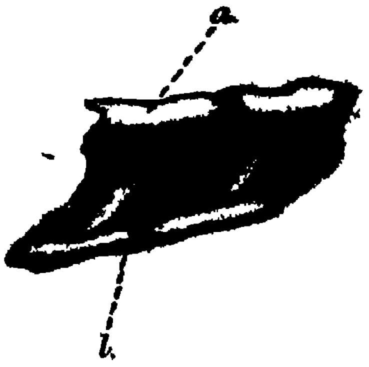

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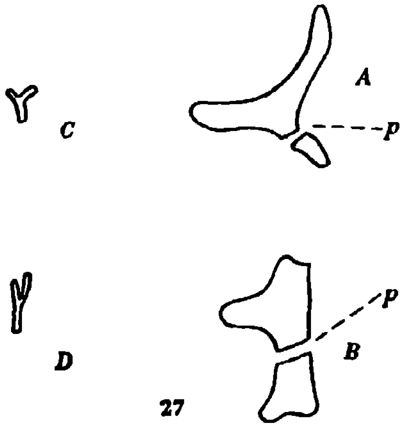

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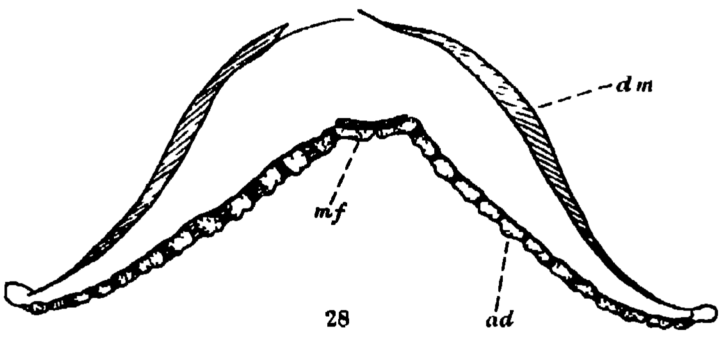

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Figure 24 *Palaeura neglecta* Schuchert Drawing of ambulacralia in oral view Main portion of ambulacral basin *b* , large proximal portion of basin, *dp* , hollow in sole of boot, the small remains of the distal portions of the basin *l* , leg of ambulacral boot

Figure 25 *Taeniaster* Portion of an arm to show the basin for the tube foot placed on one ambulacral only and the large pit *v m* , for the housing of the ventral longitudinal muscle

Figure 26*A* *Palaeura neglecta* Schuchert Side view of the aboral surface of the arm *a* , ambulacral, *l* , lateral, *M P* , mouth-angle plate

Figure 26*B* Similar view of *Drepanaster* (copied from Spencer 1940, text-fig 325*C*), showing inter-ambulacral joints, *a* , ambulacral, *l* , lateral

Figure 27 Outline of edges of basin in *A*, *Eophiura* *B*, *Palaeura* compared with the first stages in the growth of a vertebra *C*, first stage, *D*, second stage (after Ludwig 1882), *p* , pore for passage of tube foot

Figure 28 Diagrammatic arm section of an asteroid during feeding *ad* , adambulacral chain, *d m* , dorsal muscle, *m f* , mouth-frame

Superfamily Zeugophiuricae (order Zeugophiuroidea Matsumoto) with ambulacralia opposite contains families Hallasteridae Spencer, Furcasteridae Spencer, Klasmuridae Spencer and Onychasteridae Miller

Notes

The only Arenig ophiurid is a small specimen of *Hallaster* (*Hypophiura* Jaekel)

Suborder MYOPHIURINA (subclass Myophiuroida Matsumoto)

Diagnosis

Ophiurida with an enclosed ambulacral groove Palaeozoic family Aganasteridae

Subclass ASTEROIDEA

Diagnosis

Asterozoa possessing arms with thick muscular walls and a well-knit skeleton on their under surface Usually the spines are abundant and well distributed orally and aborally

The characteristic underarm skeleton has long been recognized Ludwig calls it 'the ambulacral skeleton', and so differentiates it from the remaining skeleton which he calls (following Sladen) the ambital skeleton It is formed around a well-marked ventral groove (the ambulacral groove) The floor of the groove is occupied by ambulacralia which are elongate laterally and walled by stoutly built ossicles (adambulacralia) These latter are placed in linear series upon shelves formed on the outer extensions of the ambulacralia (figure 11, p 104)

Significance of the ambulacral skeleton

Mechanisms associated with both the floor of the groove and the walls play an important part in the arm activities Those associated with the floor of the groove have been thoroughly investigated by Smith (1937, 1946) These include

(1) The tube feet Each tube foot is an antonomous organ, 'and as such, must possess its own sensory-motor reflexes In its normal functioning, however, a podium does not react independently of its fellows, and there is in the starfish a degree of co-ordination of movement sufficient for the performance, in conjunction with muscle action within the body of the animal, of the complicated movements necessary for the righting reaction or for the more normal actions of the animal in its every day life' (Smith 1937, p 130)

(2) Nerve elements, including a well-developed sensory system (ectoneural) present on the tips of the tube feet and the floor of the groove, including the radial cord, a motor system hyponeural (Lange's nerve) and association ganglia lying in cable-like tracts within the radial cord communicating with a central nerve ring, the directing centre of the animal's activities

(3) Muscle elements, transverse muscles uniting the ambulacralia of opposite sides of the arm and serving to widen or narrow the groove These movements are associated with the protrusion and retraction of the tube feet

It is the association of these elements which allows combined movements of groups of tube feet and arm musculature (see observations of Jennings quoted p 126)

The following suggestion is made upon the ossicles of the walls of the groove These seem to be arranged as a resistant to disruptive forces such as may occur when feeding upon mollusca (the favourite food)

Figure 28 gives a diagrammatic cross-section to illustrate the forces involved The starfish has raised the middle of its body to place itself over its prey The structure then is approximately that of a dome The tensions produced by the pull of the tube feet, during the opening of the bivalve shell, are very considerable Unless they were resisted the dome would collapse The resistants on the lower-arm surface are longitudinal muscles, short muscles placed between the adambulacralia, a combination of tension elements with compression elements as used in reinforced concrete which together form 'adambulacral chains' The resistants on the upper-arm surface are the dorsal muscle bands These are firmly attached to each other in the centre of the roof of the dome A further resistant is the ring of ossicles around the mouth (the mouth frame), which serves for the attachment of the adambulacral chains It seems probable that the above muscles contain elements capable of resisting muscle fatigue

The ambulacral skeleton and classification

The Palaeozoic Asteroidea can be classified according to the various characters shown by the components of the ambulacral skeleton and the neighbouring buttressing skeleton (arm axils plus marginal frame)

Order PLATYASTERIDA nov

The adambulacralia and ambulacralia are almost in one plane and the adambulacralia fail to form a well-defined wall to the groove The oral surface of the arm is broad and flat There is one family, Platanasteridae Spencer

Order HEMIZONIDA nov

The adambulacralia form a defined wall The buttressing skeleton is confined mainly to the arm axils and the ambulacral skeleton is the main arm skeleton There are two sub-orders

Suborder GNATHASTERINA nov

With conspicuous mouth-angle plates with the families Taeniactinidae Spencer, Palasterinidae Gregory and Schuchertiidae Schuchert

Suborder URASTERINA nov

With inconspicuous mouth-angle plates, with families Cnemidactinidae Spencer, Urasterellidae Schuchert and Arthrasteridae Spencer

Order PHANEROZONIDA (Phanerozonata of Sladen)

The adambulacralia form a well-defined wall The buttressing skeleton is very conspicuous and tends to dominate the ambulacral skeleton

Suborder PUSTULOSA nov

With undifferentiated spines placed on pustules With the families Petrasteridae nov, Hudsonasteridae Schuchert, Promopalaeasteridae Schuchert, Palaeasteridae Schuchert and Xenasteridae Schondorf

Notes

1 The earliest known asteroid is *Petraster* [*Uranaster*] *ramseyensis* Hicks (described Spencer 1918) It is from the Lower Arenig of Ramsey Island, south Wales A near relative occurs in the Upper Arenig of Osek Other Osek asteroids include a '*Hudsonaster*' and two small asteroids, possibly *Palasterina* and *Urasterella*

2 Comparative studies show that supero-marginalia arise independently of the infero-marginalia, and that these latter are the true buttressing frame in the early forms The beginning of the differentiation of the supero-marginalia from the skeleton of the aboral surface is well shown by *Petraster*

3 Mouth frames with deep radial V's are well shown by members of the Platyasterida and Gnathasterina The mouth frame of early Phanerozonida, e g *Petraster* and *Siluraster*, shows a V, but only between the first pair of proximal ambulacralia

4 A calcified madreporite is often absent in the fossils When present it is placed on the oral surface near the edge of the body both in the Platyasterida and the Gnathasterina, and then is a very large flat plate I am unacquainted with any observations upon recent starfish which would explain the anomalous position and size

In the two remaining orders the madreporite is in an aboral interradius In the Phanerozonida it is associated with a ring of five primary interradialia, exactly as is customary in recent Asteroidea (either in developmental stages or in the adult)

5 One genus, *Petraster* Billings [*Uranaster* Gregory], is placed in the Petrasteridae, and the Palasterinidae is confined to one genus, *Palasterina* McCoy

Characters associated with burrowing

Paxillary spines

Many fossil Asteroidea appear to have lived under the sea bottom Evidence for this is afforded by the presence of paxillae or an epiproctal cone

Gemmill (1915) has shown that centrifugal currents created on the surface of spines keep the epidermis free from debris, an operation necessary for epidermal respiration The arrangement of the aboral spines of *Astropecten* is specially adapted for respiration when the starfish retires under the sea-bottom The spines, placed on shafts, form an extensive paxillary umbrella which protects the aboral surface from the overlying mud

Respiratory currents circulate under the umbrella which can be compared to the walls of a burrow The channels under the umbrella represent the space within the burrow between the animal and the walls of the burrow *Astropecten* may be said to carry the walls of its burrow upon its back It has far greater freedom to roam in search of food than have animals which must build a new 'house' every time they change their headquarters

Many early Asteroidea belonging to widely different groups carry a paxillary umbrella It is found in the Platanasteridae, Schuchertiidae and the Urasterellidae In the last group it is almost universal

Epiproctal cone

Some recent starfish have the centre of the aboral surface raised as an epiproctal cone MacBride (1906, p 496) observed that *Astropecten* could raise the centre temporarily above the surface of the sea-bottom MacBride regarded the movement as respiratory It may, however, be associated with evacuation of the considerable volume of water often taken by recent starfish, possibly during endodermal respiration (see Gemmill 1915, p 12) Examples of epiproctal structures have been given by me, especially for the early Palaeozoic Asteroidea, the Hudsonasteridae (Spencer 1916)

GLOSSARY OF NEW TERMS

Virgalia Rod-shaped ossicles present in the oral interradii of the very early starfish, the Somasteroidea

Lateralia and sublateralia A double series of ossicles present in the primitive Ophiuroidea in approximately the same position as are the side-shields of recent Ophiuroidea

Buccal slits The slits presumed to be present in the soft tissues between the radial V's of the mouth frames which led into the central opening

APPENDIX OBSERVATIONS UPON FEEDING HABITS OF RECENT ECHINODERMATA

(*a*) T GISLÉN, 'Echinoderm Studies', *Zool Bidrag Uppsala*, 1924, 9, 273–275

'A hungry *Antedon*, when not irritated, sits immovably fastened to the substratum with outstretched arms, slightly curved upwards The pinnules are spread out from the arms almost at right angles, and the tentacles, arranged in groups of three on the pinnules, are stiffly stretched out If a plankton sample or a few grains of carmine with some crab-liver is put into the water of the aquarium, the arms and pinnules at once become very active The tentacles all beat rapidly in towards the ambulacral furrow This, the margins of which generally lie pressed tightly together, opens as soon as any grains fall upon it, with a wavy movement proceeding towards or away from the mouth The mouth, only a narrow slit before, opens to its widest extent, and becomes rounded (cf figs 333, 336) After some time the tentacles straighten themselves again, but now and then, when tiny grains fasten on the papillae, the tentacles are whipped with rapid, nervous movements towards the ambulacral groove, and then again straighten out as quick as lightning Some of the groups opposite each other usually whip in at the same time towards the furrow, but one cannot observe any flexing in of the pinnules proceeding along the arms As Reichensperger (1908*c*) has shown, unicellular mucous glands open on the papillae of the tentacles Small particles are fastened to the tentacles by their secretion, and with rapid motions of the tentacles are cast into the ambulacral groove, where the ciliary current takes hold of them and carries them to the mouth

'Sensory hairs are found on the tentacles too, and it has been supposed therefore that these serve as sensory organs The function of the tentacles is probably in reality manifold first, they are certainly of considerable importance for the respiration, secondly, the mucous secretion, as is pointed out above, serves to fasten the falling grains of plankton or detritus upon the tentacles temporarily, thirdly, the sensory cilia serve presumably as some kind of organ for taste and feeling When I dropped picric acid upon them, the arms were flexed and relaxed violently, when I added a few drops of sublimate the arms were also rapidly bent and twisted, the pinnules were stretched out and the animal made swimming motions, as if to escape On a third occasion quinine sulphate + a few grains of carmine were added, the arms were waved actively to and fro, the pinnules were flexed into the sides of the arms, or rubbed against each other, or laid over the place where the drops had fallen, the arms were turned upside down, with the evident intention of getting rid of the unpleasant matter (cf Graber's statements, 1889) When old putrefying crab liver was added to the fluid containing the grains of carmine, the pinnules were flexed in towards the sides of the arms This seems to indicate that a sense of taste is present which, presumably, may be considered as localized in the sensory hairs of the tentacles' papillae

'I cannot decide with certainty whether Reichensperger's assumption is correct that the secretion of the papillae of the tentacles is poisonous, and these papillae, like the cnidoblasts in *Cnidaria*, are partly defensive organs I allowed living pinnules to lie in contact with freshly caught plankton (Ephyrae, Peridineans, Diatoms and Plutei) Nevertheless, I was not able to ascertain that any rapid unconsciousness or poisonous action took place A small *Cladonema* seemed to make motions of escaping when touched by a tentacle, but usually the tentacle bent away from the irritating object In the intestine of *Heliometra eschrichti* (see below) I have found quantities of copepods The copepods have a tolerably strong power of motion of their own, and it is very probable that in this case the secretion of the papillae of the tentacles in some way paralyses the prey Otherwise, it is difficult to imagine how the relatively weak ciliary currents can transport the captured prey to the mouth (N B however, the rudimentary combs on the proximal pinnules (cp p 287)) '

(*b*) Extracts from Blegvad Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea-bottom in Danish waters *Report of the Danish Biological Station*, **22**, 1914 (publ 1915)

P 61 'Animals feeding by means of ambulacral feet (tube feet)

'(1) Those without arms and living buried in the bottom, Echinoidea irregularia without masticatory organs (Atelostomata), includes *Brissopsis*, *Echinocardium* and *Spatangus* All these are typical detritus eaters, feeding directly on the upper layer of the bottom, without any previous sorting of the detritus As the aquarium observations have shown, they live buried in the bottom, maintaining communication with the surface by means of vertical tubes, and drawing their food by means of the far reaching ambulacral feet As already mentioned, the *Echinocardium cordatum* frequently devours, together with the bottom detritus, numbers of quite small young bivalves

'(2) Very mobile arms, living buried in the bottom *Amphiura* Two species

'The *Amphiura* species live, as I have frequently observed in aquaria, buried deep down in the bottom, only the extremities of some of the arms reaching up over it These extremities are in constant movement, feeling about over all the small particles in the vicinity, and now and again coiling round and grasping some few of them, the food being then drawn down beneath the surface of the bottom to the mouth Having noticed that *Amphiura* in aquaria would allow themselves to be fed with small pieces of meat I was for some time inclined to believe that they might, occasionally at any rate, be carnivorous, I have, however, examined several hundreds of specimens taken at different times and seasons, without ever finding anything in their stomachs beyond more or less finely sorted bottom detritus, with the micro-organisms and skeletal parts therein contained '

P 63 'It would seem most probable that both poison and mechanical suction are applied when a starfish attempts to draw out a large bivalve or gastropod '

P 64 '*Astropecten mulleri* lived for the most part on molluscs Small forms and young specimens especially are attacked by this voracious animal '

(*c*) JENNINGS, H S 'Behaviour of starfish' *Univ Calif Publ Zool* 1907, 4, no 2, pp 153–185, 19 text-figures

P 93 'There are two main methods of conveying food to the mouth Large objects are usually carried by the active bending of the ray beneath the body, till the object is applied to the mouth, as described above in our account of the capture of a crab Small pieces of flesh are transported in a somewhat different manner After being carried to the ventral side of the ray, near its tip, perhaps the ray bends downward and under at precisely the point where the food body touches it, as to bring the food into contact with a point on the lower surface of the ray nearer the disk The tube feet of this nearer point then seize the flesh while the more distal ones release it Now the point at present bearing the food bends downward, applying it to a new region, while the point first bent straightens out Thus the food is passed from one set of tube feet to another, slowly along the under side of the ray till it reaches the mouth

When the stomach is passed out of the mouth in feeding, it usually appears as five yellowish lobes or sacs These fold about the prey, partly envelop it, and insert themselves into its cavities and angles But the prey is never, so far as I have observed, actually within a sac formed by the stomach, it merely has these lobes closely applied to it '

(*d*) VON UEXKULL, J *Umwelt und Innenwelt der Tiere*, 1921 Berlin J Springer

'Die Schlangensterne' (*Ophiothrix*)

'Die Armmuskulatur beteiligt sich gar nicht am Erfassen der Beute, sondern die bei ihr besonders ausgebildeten Tentakel (siehe Hamann) schieben sich gegenseitig die kleinen Nahrungsbrocken zu, die im Zickzack von der Armspitze zum Mittelkorper wandern '

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DESCRIPTION OF PLATES 2 TO 8

PLATE 2

FIGURE 29 *Villebrunaster thorali*, n g et n sp Holotype Photograph of a cast showing two individuals lying side by side (magn × 2) The photograph to the left (the holotype) shows five arms lying in one plane (see figure 1), that to the right two arms flexed upwards (see figure 3) Coll Villebrun, Univ Montpellier

FIGURE 30 *Villebrunaster thorali* Photograph of an original mould showing impressions of the arm in aboral view and, to the right, impressions of the spicules (magn × 6) The mesh between the spicules, on the left of the photograph, is irregular Adjacent are impressions of the rows of virgalia

FIGURE 31 *Villebrunaster thorali* Photograph of another portion of a mould showing the spicular impressions (magn × 10) The mesh, in the lower part of the photograph, has hexagonal outlines

FIGURE 32 *Chinianaster levyi* Thoral Photograph of a cast of the oral surface of a small specimen (magn × 3) Coll Thoral

FIGURE 33 *Chinianaster levyi* Thoral Photograph of a cast of one angle (magn × 2) Coll Univ Montpellier Rows of virgalia are seen to the upper left of the angle

FIGURE 34 *Archegonaster pentagonus* n sp, with arms flexed upwards (magn × 1 5) Coll Mus Rokitzan

PLATE 3

FIGURE 35 *Chinianaster levyi* Thoral Lectotype Photograph of a cast of the oral surface (magn × 1 75) Coll Villebrun, Univ Montpellier The structure of an interradius is seen lower right

FIGURE 36 *Chinianaster levyi* Thoral Photograph of a cast of the aboral surface of the same specimen (magn × 1 75) A spicular net covers the centre of the body, exposed ambulacralia are seen in the lower arm

FIGURE 37 *Archegonaster pentagonus* n sp Photograph of a cast of the oral surface (magn × 1 75) Coll Narodni, Mus Prague, E H 30 The virgalia are confined to the distal arm regions The rounded ossicle with a central depression seen in the lower left interradius is the madreporite Above it are seen the dislocated ossicles of the stone canal

FIGURE 38 *Archegonaster pentagonus* Aboral surface (about nat size) Specimen L H 36 The marginal frame is drawn inwards slightly (lower right) and sharply (upper left)

PLATE 4

FIGURE 39 *Archegonaster pentagonus* n sp Holotype Photograph of a portion of the oral surface (magn × 4) Coll Narodni, Mus Prague, E H 7 The adambulacralia on the right arm carry tufts of spines They have swung outwards exposing the wide ambulacral channel and the basins for the tube feet (See also figure 54, plate 8 and figure 10, p 104)

FIGURE 40 *Archegonaster pentagonus* Photograph of the counterpart of the same specimen showing the aboral surface (magn × 4) The upper surfaces of the ambulacralia are well exposed (See also figure 13, p 104)

PLATE 5

FIGURE 41 *Pradesura jacobi* (Thoral) Lectotype Oral surface of the disk and the arm bases (magn × 2 6) Coll Univ Montpellier, no 139 (mould of this specimen figured, Thoral, plate ix, figure 2)

Figure 42 *Pradesura jacobi* (Thoral) The same view of a second specimen (magn × 3 5) Same collection, no 138 (mould figured, Thoral, plate ix, figure 3*a*) Spines are seen near the disk margins in the upper left-hand interradius

Figure 43 *Pradesura jacobi* (Thoral) The same view of a third specimen (magn × 1 75) Same collection, Px The lateralia have revolved inwards and partially closed the groove

Figure 44 *Pradesura jacobi* (Thoral) Aboral surface of same specimen Px (magn × 1 75) The aboral surfaces of the exposed ambulacralia show small ball and socket joints

Figure 45 *Pradesura jacobi* (Thoral) Aboral surface of another specimen (magn × 1 75) Same collection, no 137 The mouth frame is widely open and crushed through the aboral covering

Plate 6

Figure 46 *Eophiura bohemica* Schuchert Lectotype Oral surface of the disk and the arm bases (magn × 2) The madreporite is in the upper right-hand interradius lying alongside the mouth frame Coll Narodni Mus Prague, no E H 94

Figure 47 *Eophiura bohemica* Schuchert Madreporite and stone canal of same specimen (magn × 9)

Figure 48 *Eophiura bohemica* Schuchert Ambulacral basins at the base of the buccal slits from same specimen (magn × 6) The upper ossicle shows a groove at the distal end of the basin, the second ossicle a groove at the proximal end of the basin

Figure 49 *Eophiura bohemica* Schuchert Aboral surface showing exposed ambulacralia and buccal slits, defined by a light wash, natural size Same collection, E H 105

Plate 7

Figure 50 *Eophiura bohemica* Schuchert Photograph of a cast of ambulacralia showing the tears in the cast by the hardened infillings of the branch vessels (magn × 6) Coll Narodni Mus Prague, E H 98 The tears between the ambulacralia to the left are shown clearly

Figure 51 *Eophiura bohemica* Schuchert Oral surface of the distal extremity of an arm (magn × 10) Specimen no E H 97 Sub-lateralia are seen to the lower left

Figure 52 *Eophiura bohemica* Schuchert Lateralia showing spine attachments and spines (magn × 10) Specimen no E H 110

Figure 53 *Eophiura bohemica* Schuchert Scales of the oral surface of the disk (magn × 6) Specimen no E H 94

Plate 8

Figure 54 *Archegonaster pentagonus* n sp Ambulacralia (right) and adambulacralia (left) (magn × 6) Coll Narodni Mus Prague, E H 11 The adambulacralia have swung open Their stalks and the ambulacral-adambulacral narrow joints are seen upper left

Figure 55 *Archegonaster pentagonus* n sp With arms flexed over disk (magn × 1 5) Another photograph of the specimen shown in figure 34

Figure 56 *Eophiura bohemica* Schuchert Three arms flexed over the aboral surface (magn × 1 5) Coll Narodni Mus Prague, E H 101 The oral surfaces of the arms are exposed and the tube feet were in position to feed from the contents of the overlying mud

Figure 57 *Eophiura bohemica* Schuchert The mould of two arms flexed steeply to the disk with the water vessels infilled with hardened mud The infilling of the radial vessel is along the middle of the arm and on each side are the infillings of the short branch vessels and the round bases of the tube feet (magn × 1 5) Specimens no E H 100

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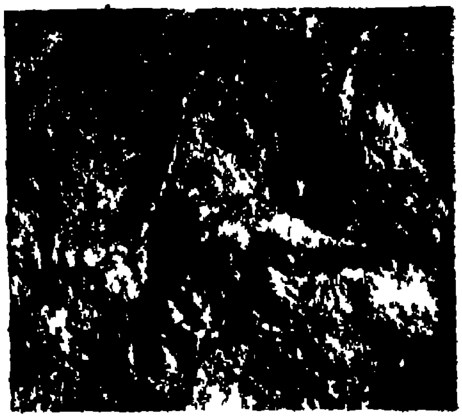

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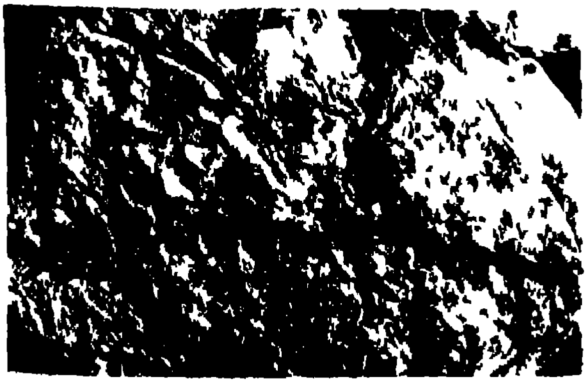

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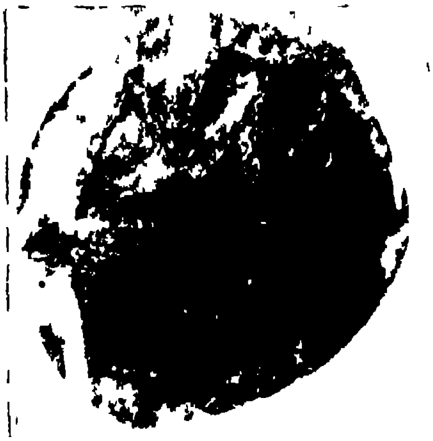

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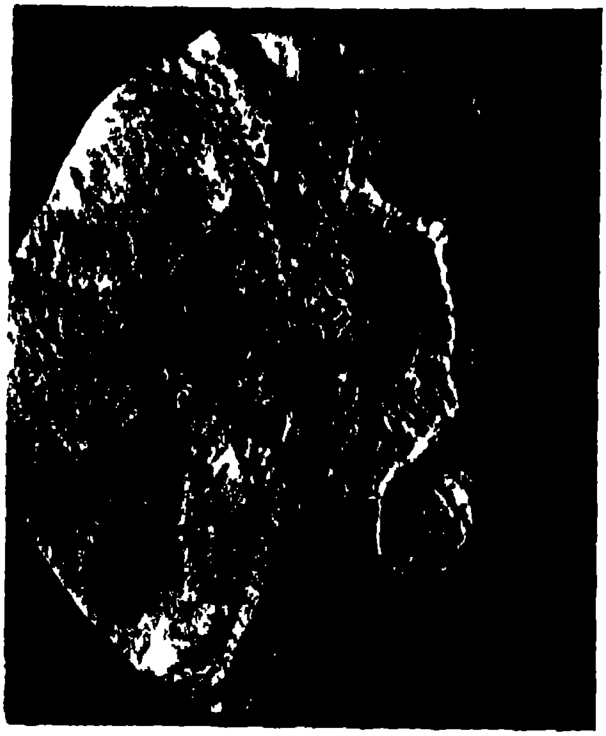
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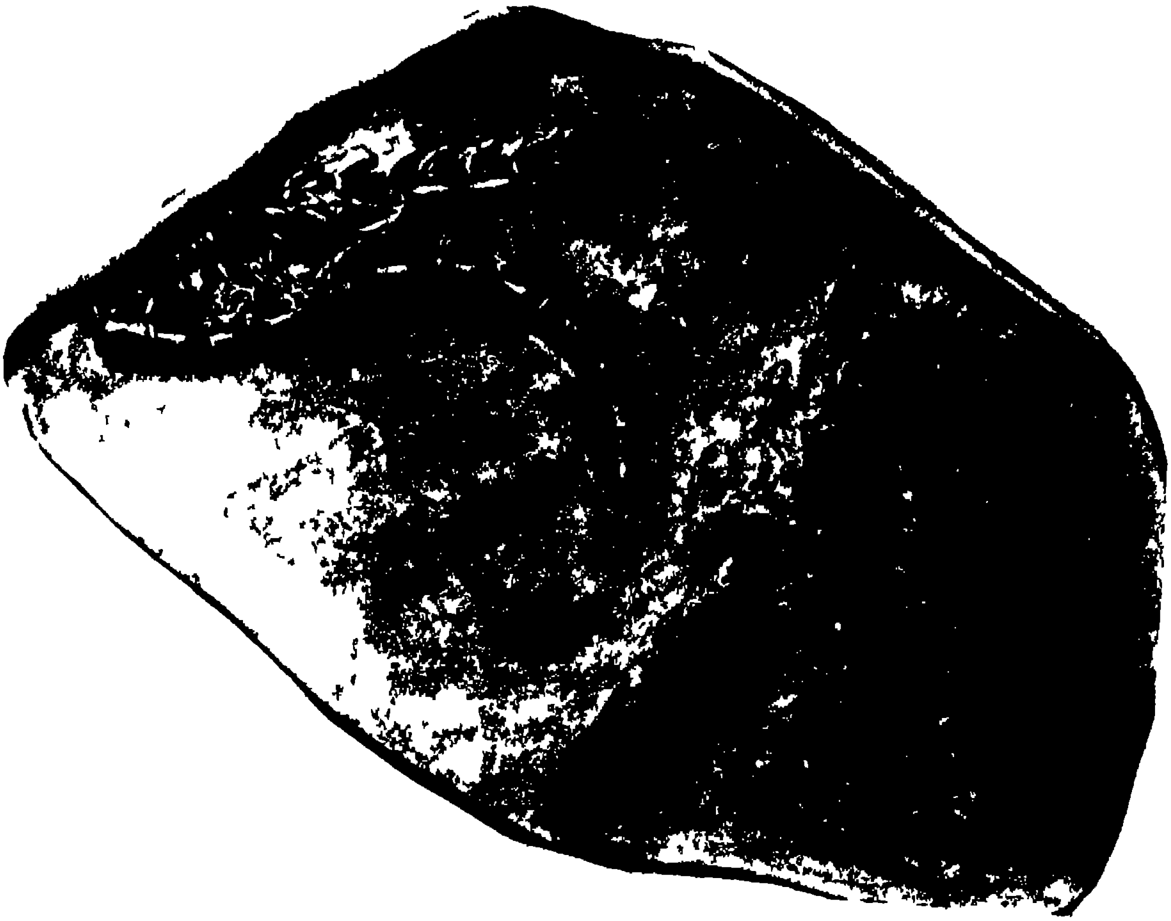

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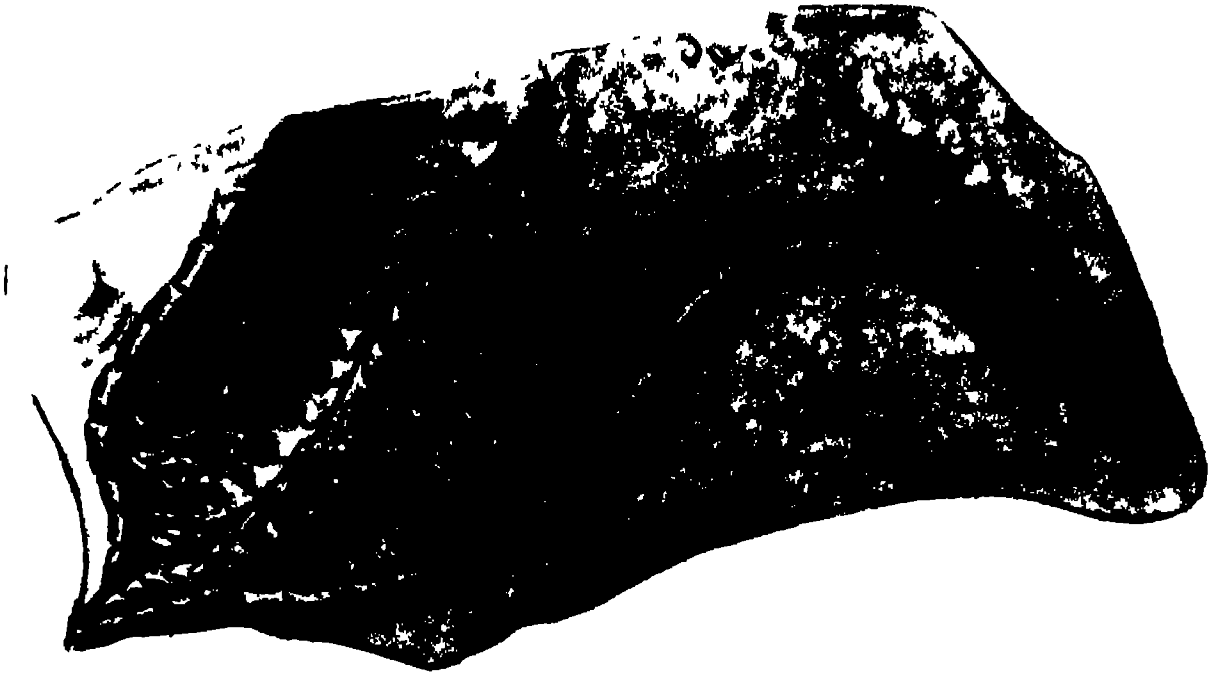

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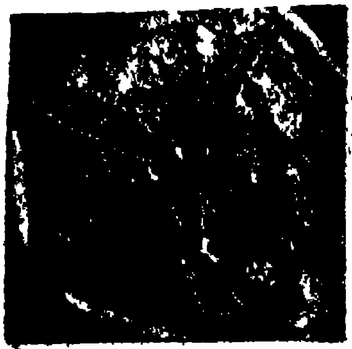

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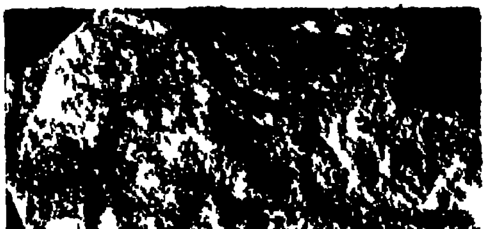

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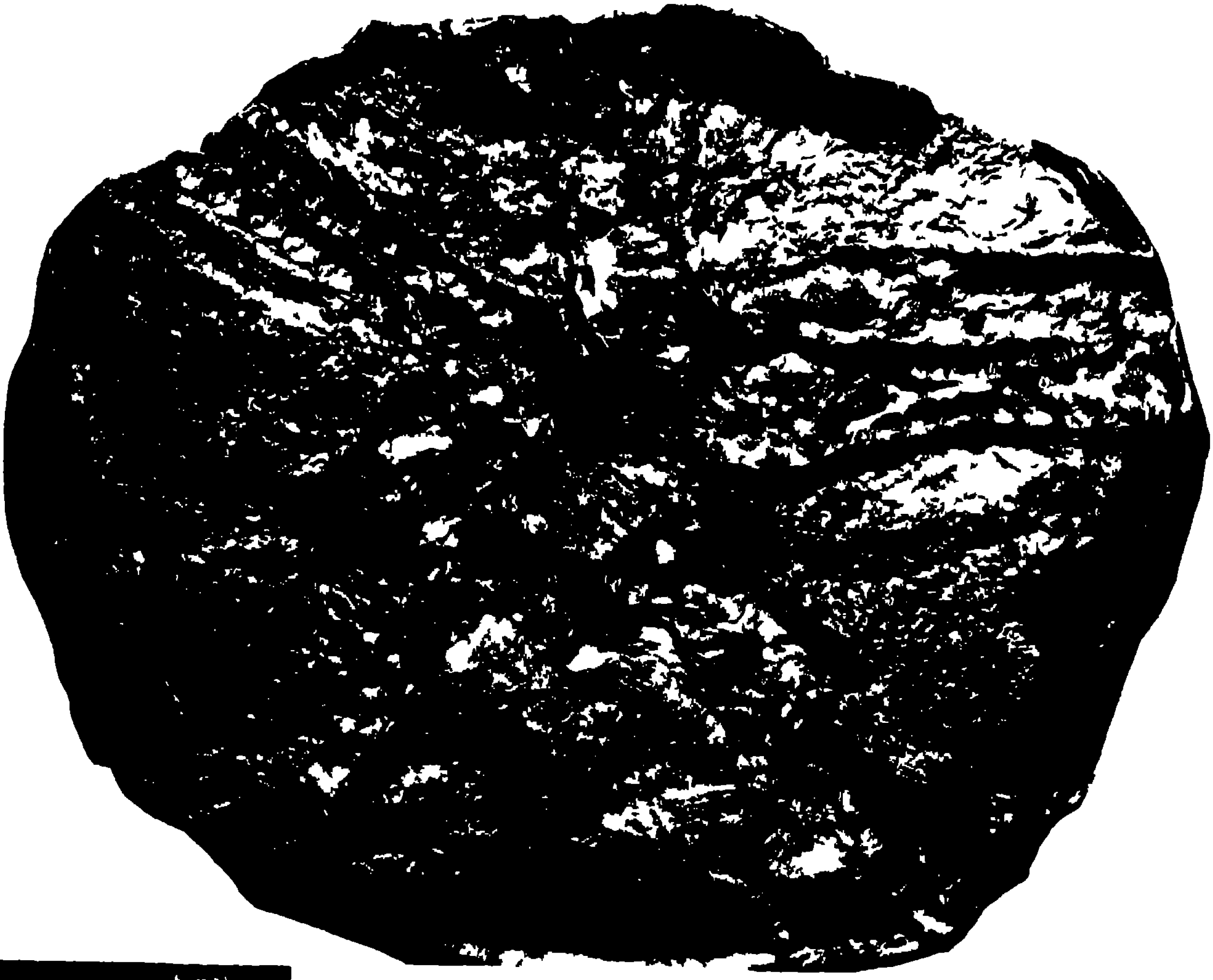

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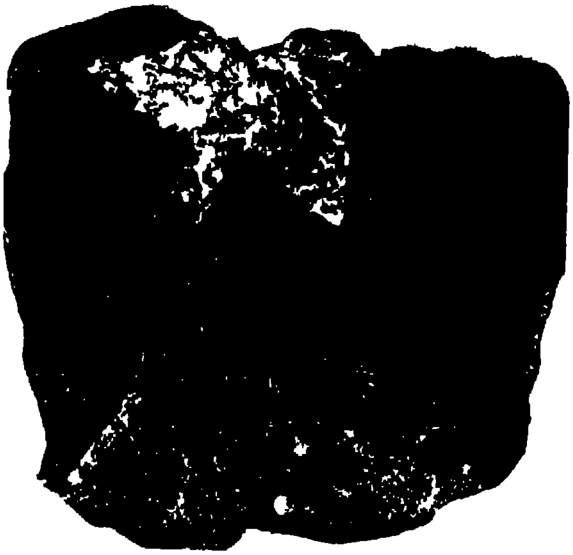

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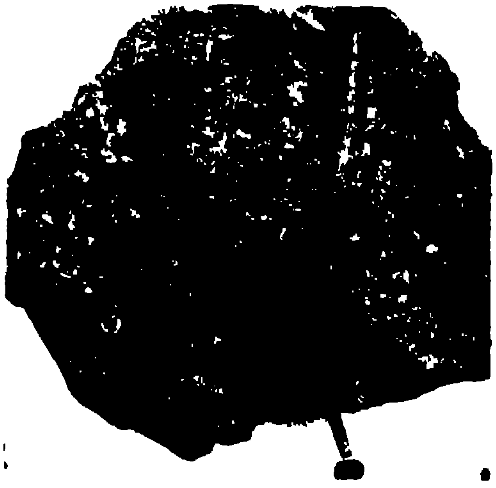
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EXPERIMENTS ON SPIRODISTICHOUS SHOOT APICES I

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(*Communicated by R. Snow, F.R.S.—Received* 9 *March* 1950—*Revised* 22 *June* 1950)

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The shoot apex of *Rhoeo discolor*, a spirodistichous species, is described in detail. The mean divergence angle between successive leaf centres is 152°·6. Each new leaf covers only a small arc when first visible, and its flanks then extend round the apex until they meet in the later part of the plastochron. The new leaf is asymmetric, its half which is anodic in the direction of the genetic spiral being the shorter transversely and covering a mean arc of 166°·5 when the flanks meet. Thus the centre of a new leaf does not lie directly over the meeting-point of the flanks of the previous leaf, but above its anodic half.

Experiments were made in order to discover the causes on which the divergence angle depends. As a preliminary some stem apices of *Rhoeo* were exposed and marked with transverse streaks of albumen and charcoal. But after several days the streaks had not been bent by the growth of the apex in the way which would be expected on Hirmer's theory of spiral growth.

In the main experiments the central part of P_1, the youngest leaf, was cut out completely. It was necessary first to cut down P_2 and the older leaves of the bud nearly to their bases. The main results were that I_1, the next leaf to arise, was displaced towards the missing centre of P_1, and that the angle I_1-I_2 was larger than the normal, and sometimes exceeded 180° (see figure 6). In some other experiments the central part of P_2 was removed as well as that of P_1. In these also the angle I_1–I_2 increased, and in one of them the genetic spiral reversed permanently, but the displacement of I_1 towards P_1 was usually less.

It is concluded that the position of the centre of each new leaf depends on a balance between inhibiting influences exerted on the stem apex by existing leaf centres. The position of a new leaf *n* depends mainly on the inhibitions coming from the centres of the two youngest leaves, *n*–1 and *n*–2, and to a lesser degree on those from the centres of *n*–3 and possibly *n*–4. The strength of the inhibition thus decreases with the age of the leaf from which it comes and also with the distance from the inhibiting centre.

The asymmetries of the leaves that arose after the operations are reported and discussed in comparison with those of the normal leaves. Many of the facts can be explained if it is supposed that the same influences from existing leaves which tend to inhibit the formation of leaf centres

VOL. 235. B. 624. (Price 7s. 6d.) 18 [Published 16 January 1951

promote the extension of leaf flanks round the apex But the asymmetry of I_3 in most of the experiments is at present not explained on this hypothesis

The localization and determination of leaves in *Rhoeo* is further discussed and compared with the corresponding processes in *Lupinus albus* and other dicotyledons It is concluded that in spirodistichous monocotyledons the localization of leaves, depending on physiological inhibitions, is different from what it is in dicotyledons, in which it was previously concluded to be a space-filling process The process of determination is also shown to be different in *Rhoeo*, since a rather small central part of a leaf is determined first, and from it the determination extends by induction round the apex In both these respects the experiments on *Rhoeo*, unlike those on dicotyledons, give good support to Richards's theory of phyllotaxis, which, however, was intended to apply to all groups

INTRODUCTION

The phyllotaxis of monocotyledons has received less attention than that of dicotyledons and no experimental work has been done on them The majority of monocotyledons have straight distichous phyllotaxis, and most of those which have spiral phyllotaxis have systems of the kind which is called spirodistichous, and not Fibonacci spirals Spirodistichous systems, according to Hirmer (1922), occur in species belonging to the families Liliaceae, Juncaceae, Bromeliaceae, Araceae, Commelinaceae and Hydrocharitaceae, they are usually derived from distichy in ontogeny, the first leaf of the seedling being opposite the cotyledon, and the change to spirodistichy may occur at the second leaf or later When this happens the leaves are laid down with a divergence angle of less than 180° but considerably greater than the Fibonacci angle of 137° 5 which is closely approached by most dicotyledons with spiral phyllotaxis In consequence of this decrease of the divergence angle the two orthostichies become helices instead of straight lines If the angle falls very much below 180° the two helices are no longer apparent to the eye

The biological value of spirodistichy may well be that it exposes the leaves more fully to light than does straight distichy, for most spirodistichous types have short internodes, at least during a large part of their growth, and so would receive much less light if their distichy were straight

A significant feature in which spirodistichous systems differ from the spiral systems of dicotyledons is that each young leaf covers an arc of more than 180° before the next leaf arises, not only in the young seedling, but also later Indeed, to judge from the drawings given by Hirmer (1922) in many spirodistichous species each leaf encircles the whole apex before the next leaf arises Thus the change in divergence angle in spirodistichous systems does not depend on a change in the arc covered by each young leaf, whereas in the seedlings of dicotyledons the changes in the divergence angle regularly do depend on changes in the arcs of the leaves The divergence angles in spirodistichous plants vary considerably from one species to another It has also been claimed that the angle varies considerably within a species or in a single plant, but it will be shown that this variation is not always so great as is supposed Another feature in which the spirodistichous systems of monocotyledons differ from most spiral systems of dicotyledons is in the asymmetry of the leaves This asymmetry is not always obvious in the blade of the mature leaf but can usually be seen in transections through the bud, where it appears that the morphological 'median' strand of the leaf divides the leaf into two lateral parts which differ in tangential extension and sometimes in radial thickness

From these facts it is clear that the hypothesis of the first available space cannot easily be applied to spirodistichous plants According to this hypothesis 'each leaf arises in the first space that becomes both wide enough and far enough below the growing point' (Snow, M & R 1931, p 16 and 1933, p 360) This hypothesis is based on the theory of van Iterson (1907) and has been supported by various experiments (Snow, M & R 1931, pp 33, 35) Van Iterson's theory was in turn based on Hofmeister's observation (1868) that each leaf arises in the largest gap between the previous leaves But van Iterson expressly stated that his theory could not be applied to plants with asymmetric leaf bases since he had worked it out only for plants in which the bases of the youngest leaf primordia were circular in outline

Schumann (1892,) however, did attempt to apply Hofmeister's rule to plants with spirodistichous phyllotaxis He maintained that the greatest available space in plants with sheathing leaf bases was to be found immediately above the point where the edges of the sheath of the youngest leaf met (p 34) Where the leaves were symmetric this point lay opposite to the centre of the youngest leaf and distichous phyllotaxis resulted But when the leaves were asymmetric this point was not opposite to the morphological centre of the youngest leaf, and spirodistichous phyllotaxis resulted (p 42) The asymmetry of the leaves was thus taken by Schumann to be the determining factor in the phyllotaxis and was considered to be a basic inherited character This theory meets with the difficulty that an asymmetry of either the one sense or the other is supposed to be inherited, though it is not determined by heredity of which sense that asymmetry will be A further and more serious difficulty is that in many spirodistichous plants, and probably in all, the centre of each new leaf does not lie immediately above the point where the edges of the previous leaf meet, but slightly to one side of this point, as can be seen from Hirmer's figures (1922) illustrating a wide range of types Moreover Schumann himself according to Weisse (1932, pp 340–341) later abandoned his attempt to explain spirodistichous phyllotaxis in accordance with Hofmeister's rule

The theory of Hirmer must next be considered According to Hirmer spirodistichy is derived from distichy in ontogenesis through the shifting of the plane of symmetry of the apex by unequal growth on each side of the plane (pp 17–19 and figure 46) The plane of symmetry here referred to is the median plane of the youngest leaf In consequence of this asymmetric growth a sector is inserted in the apex in such a way that the centre of the next leaf which is about to arise is displaced to one side of the median plane of the previous leaf and a new plane of symmetry is established This process is repeated each time that a leaf is formed

The terms 'anodic' and 'kathodic' are used by Hirmer, and by Troll (1937) following him, with reference to the direction in which this shift of the leaf centre is supposed to have taken place The anodic side of the leaf on Hirmer's terminology is the side towards which the centre is supposed to have shifted, and this is in the opposite direction to that of the genetic spiral But since this shift of the leaf is only assumed and has not been proved to occur, it seems to the writer better to use the terms anodic and kathodic with reference to the direction of the genetic spiral, as this is the accepted convention for other phyllotactic systems The side of each leaf which Hirmer calls 'anodic' is thus in the present terminology 'kathodic', since it lies next to the centre of the next lower, that is older, leaf The symmetry of the leaf bases is considered by Hirmer to support his theory, for he claims that the side of the leaf termed 'kathodic' by him ('anodic' by the writer) is the larger, since it occupies the region in which the apex has grown most strongly, and is the side which has been, so to speak, left behind by the displacement of the leaf centre In support of this contention he illustrates bud sections of many spirodistichous plants In some of these plants, e g *Cordiline rubra*, *Richardia podophyllum* and *Tillandsia stricta*, this side does indeed appear to be the thicker radially in cross-section, but the figures do not provide evidence that it is the longer in tangential extension, as would be expected if the increase of growth was in the tangential direction as he postulates, for few of the sections illustrated pass through the critical level at which the meeting-point of the edges of the leaf can be seen, and these few are reproduced on too small a scale to allow of accurate measurements Moreover in *Pollia condensata*, which is spirodistichous, Hirmer admits that the sides of the leaf are equal in size, and it will be shown in the present paper that in *Rhoeo discolor* the difference in the tangential extensions of the flanks is actually the opposite

Hirmer has produced no evidence for his theory that a sector is inserted in the apex apart from this claim concerning leaf asymmetry which is unconvincing for the reasons given Yet this theory has been included by Troll in his *Vergleichende Morphologie* (1937) as if it were well established, and a similar process is considered by Hirmer and by Troll to account for the spiral phyllotaxis of dicotyledons also

Some observations on marked apices made to test Hirmer's theory will be briefly reported before the main experiments Since the results of these marking experiments were negative, and since the study of spirodistichy by observation alone had failed to provide a satisfactory basis for it, it seemed to the writer that operations on the apices were needed for the purpose, and the results of such experiments will be reported and discussed in the present paper

Rhoeo discolor was the species chosen for investigation because it was found to be the least inconvenient species to dissect and to withstand the operations well A further advantage is that the whole species shows very little genetic variation

THE NORMAL APEX AND PHYLLOTAXIS OF *RHOEO DISCOLOR*

The majority of the plants used in the experiments were young cuttings of *R discolor* struck from basal buds in early spring, seedlings were also used after 12 to 14 leaves had been formed Since the internodes elongate very little the apices of the operated plants were fairly close to ground level The stem is completely encircled by the sheathing bases of the leaves which form closed tubes for a short distance above their insertions

In order to determine the divergence angle the apices with seven or eight of the youngest leaves were embedded in collodion and sectioned by hand or with a microtome, and the sections were drawn under a projection apparatus The angles were measured on the drawings The centres of the leaves were located by the positions of their median conducting strands, which in *Rhoeo* are differentiated at an early stage The median conducting strand was usually visible even in the youngest leaf The centre of the axis was more difficult to determine and was judged by eye as accurately as possible In order to allow for errors in determining the centre of the axis each divergence angle was measured in at least three

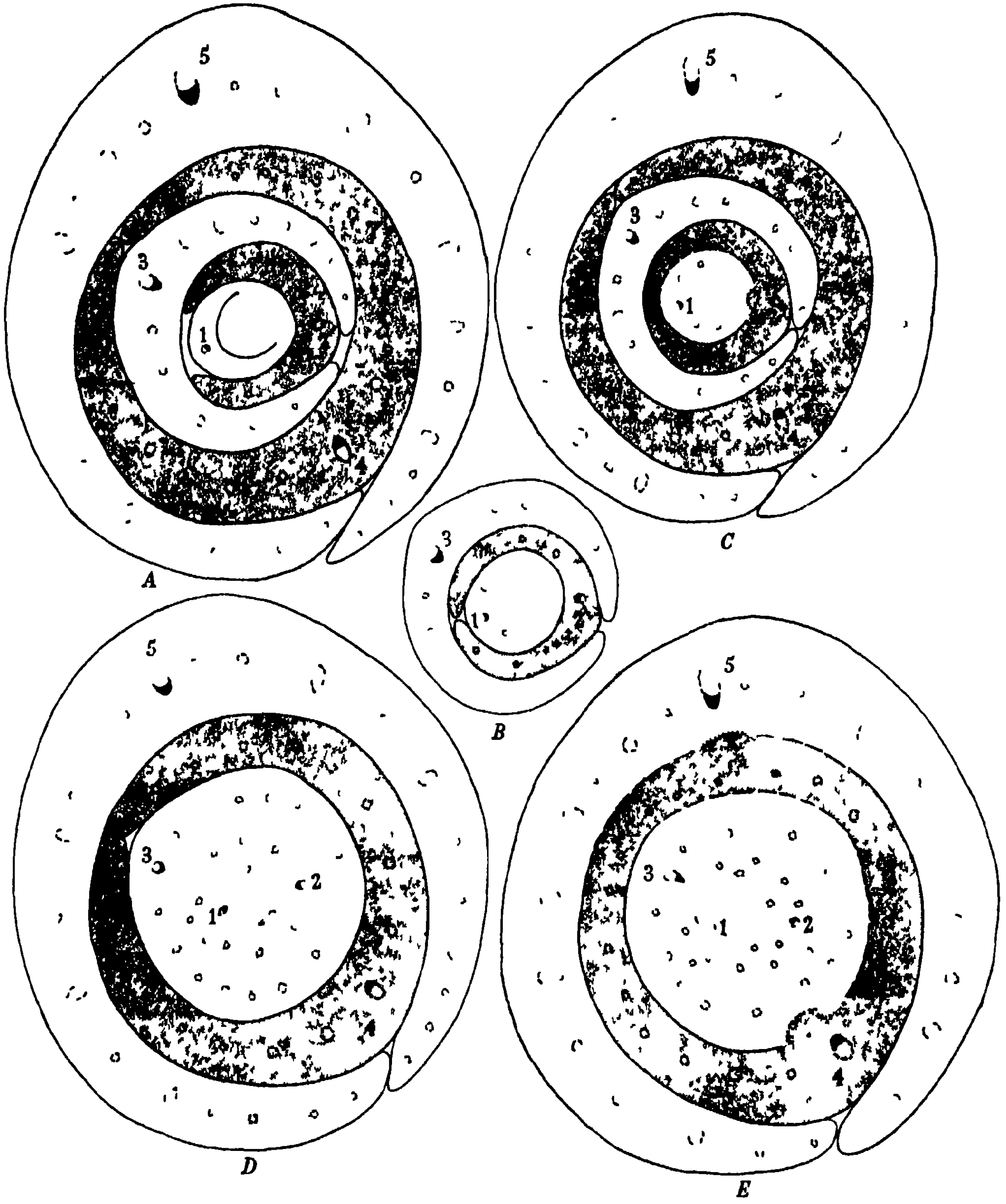

FIGURE 1 *A* to *E* are transections through the apical region of a normal plant of *Rhoeo discolor* from above downwards In this and all subsequent figures vascular and procambial strands are shown with broken lines and the xylem regions of the central strands are shown black The leaves and their axillary buds are shown alternately clear and stippled to guide the eye The boundary between leaf and axis at the insertion level of a leaf is shown with long broken lines, and the region immediately beneath an axillary bud is enclosed within a dotted line (Magn *A*, × 58, *B*, *C*, *D* and *E*, × 52)

sections taken from different levels and the average was found This method could not always be applied to the youngest leaf, the central conducting strand of which was sometimes seen in only two sections so that two measurements had to suffice The same procedure was usually adopted in the experiments reported below Fourteen different plants (cuttings) were used for measurements of the divergence angle, and the total number of divergence angles measured was 76 The mean value of these angles was 152° 6, the extremes were 142° 2 and 161° 7 The standard deviation was 3° 7 and the standard error was 0° 42 This indicated that the variation of the divergence angles in this species is by no means so great as it is often stated to be in spirodistichous plants For comparison the standard deviation of the divergence angle of *Lupinus albus* with Fibonacci phyllotaxis was found to be 2° 8 (Snow, M & R 1931) Transections of the apical region of a normal plant of *Rhoeo* are shown in figure 1 Four lateral strands were visible in the youngest primordium before the end of its first plastochron Other strands were added later and these appeared to differentiate acropetally, new strands being inserted between older ones, so that large and small strands usually alternated The median vascular strand was found to run nearly straight downwards for at least four internodes before uniting with the lateral strand of another leaf The direction of differentiation of the central strand when it first appeared was not determined, but its subsequent differentiation within the leaf was seen to be acropetal, as it kept pace with the upward growth of the leaf

Each leaf subtends an axillary bud, and the area from which the bud will develop is clearly visible in the axil of the second youngest leaf as a small group of cells with dense contents The bud is seen as a definite protuberance in the axil of the fifth or sixth leaf, and it then becomes quite clear that it does not lie in the median plane of the leaf, but that its centre lies on a radius a few degrees anodic to that of the median strand Its relationship to the median strand enabled the latter to be identified in a few leaves of the operated plants in which the median strand was scarcely larger than the lateral strands The cells lying immediately beneath the insertion of an axillary bud were distinguished from the surrounding tissues by their dense contents In the drawings these groups of cells with dense contents are enclosed within dotted lines

As transections do not give a satisfactory representation of the shape and course of development of the youngest leaf, an attempt was made to draw the apex and the youngest leaf as seen in surface view from above through the dissecting microscope at different stages of the plastochron The drawings were made free-hand and are reproduced in figure 2 The direction of the genetic spiral, from each leaf to the next younger, was clockwise in the four apices shown in figure 2, and the terms anodic and kathodic will be used with reference to this spiral The same terminology will be used as in previous papers (Snow, M & R 1931, 1933, 1935) the leaf primordia visible at the time of operation, will be called P_1, P_2, P_3, etc , P_1 being the youngest, those arising after the operation will be called I_1, I_2, I_3, etc , I_1 being the first to arise In figure 2, though no operation has been made, the youngest primordium will be referred to as P_1 Each drawing in figure 2 is accompanied by an outline drawing of a longitudinal section of the apex at the same stage of the plastochron In figure 2A_2, B_2 and C_2 these sections pass through the median plane of P_1, in D_2 the section passes through the region which is about to give rise to I_1 The longitudinal sections were cut under the dissecting microscope from apices prepared in the

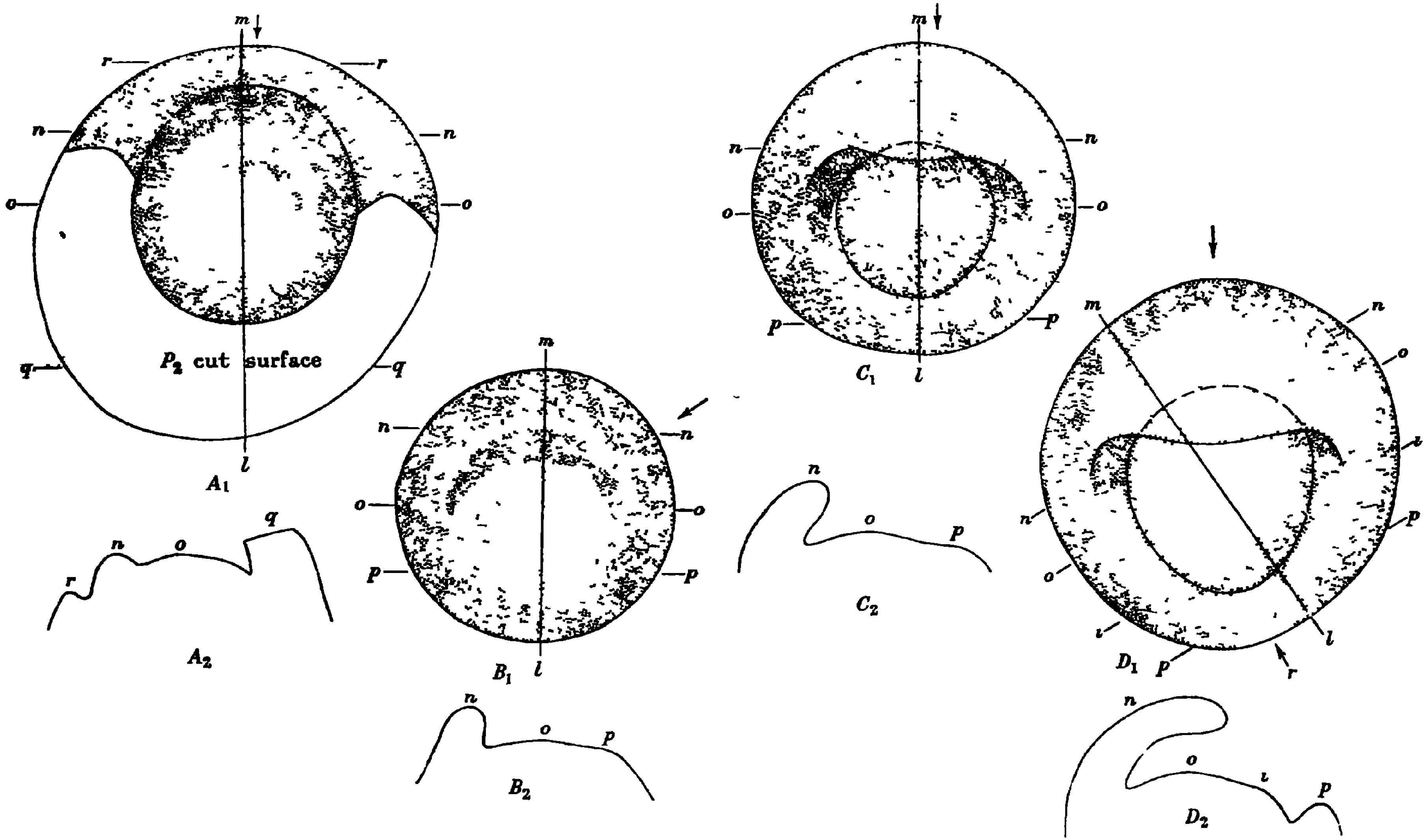

FIGURE 2 A_1, B_1, C_1 and D_1 are free-hand drawings of the apex viewed from above at different stages of the plastochron The source of light was obliquely above the apex, and the arrows indicate the horizontal component of its direction Horizontal and slightly oblique surfaces are illuminated, surfaces approaching the vertical are shaded A_2, B_2, C_2 and D_2 are longitudinal sections through the plane *m* to *l* shown on the corresponding drawings, × 130 The base of P_2 which has been cut down is included in figures A_1 and A_2 only The points in which the lines *n–n*, *o–o*, etc , cut the line *m–l* in the drawings *A* to *D* are indicated with corresponding letters in the sections A_2 to D_2 *n* = summit of P_1, *o* = summit of apex, *p* = flanks or presumptive area of flanks of P_1, *ι* = foliar buttress of I_1, *q* = cut surface of P_2 In A_1 and A_2, P_1 is small In B_1 and B_2, P_1 is small-medium, the shaded lines represent cell rows in the region from which the flanks of P_1 will arise In C_1 and C_2, P_1 is medium, the hood is beginning to arch over the apex In D_1 and D_2, P_1 is very large The arrow marked *r* indicates the meeting-point of the edges of the flanks The broken line shows the contour of the apex beneath the hood usual way as if for operations (p 139) to ensure that the stage of the plastochron was the same as that shown in surface view and that the cut passed through the correct plane They were drawn under the projection apparatus

When P_1 is first visible as a protuberance it subtends an arc of about 90°, and by the end of the first plastochron it has encircled the whole apex, and its central region has by then made a hood which arches over the apex and partly conceals it, as is shown in figure $2D_1$ Those parts of the leaf which extend round the apex as distinct from the original central part will be called 'flanks' For convenience the anodic and kathodic parts of the leaf which lie between the centre and the meeting-points of the flanks will be called the anodic and kathodic 'halves' though they are slightly unequal in size, they may be considered as morphological halves A half of a leaf is thus more than a flank, as it comprises half of the central region as well as one flank

Figure $2A$ shows P_1 at a fairly early stage of its development The flanks of the leaf have extended until it covers an arc of nearly 180°, and the apex appears as an approximately circular dome In figure $2B_1$ the arc is slightly greater than 180°, and the region into which the flanks will extend is differentiated from the rest of the apex as an annular region extending for nearly 180° round the apex In this region curved cell rows are clearly visible P_1 is slightly asymmetric, its anodic half being rather the taller and rising up more steeply than the kathodic half In figure $2C_1$, P_1 has developed considerably further, and its central part has formed a hood which arches over the apex and partly conceals it Incidentally, the growth rate of the hood relative to that of the flanks showed some variation, for in some halves the flanks had already met round the apex when the hood had scarcely begun to arch over In figure $2D_1$ a later stage is shown in which the flanks have met round the apex The point in which they meet is clearly not opposite the centre of P_1, so that P_1 is asymmetric, its kathodic flank being the longer

At a later stage the edges of the flanks unite and form a short tube as shown in figure $1D$, leaf 4, above this tubular region the edges of the flanks continue to extend tangentially and overlap as shown in figure $1D$, leaf 5, the anodic flank being the outer It should therefore be noted that the overlapping of the flanks takes place only in the part above the basal tube

A further point of interest seen in the dissections was the change that took place in the shape of the apex during the plastochron Thus in figure $2A_1$, B_1 and C_1, the apex appears as an approximately circular dome, but in figure $2D_1$ it is clearly elongated along a diameter passing through the centre of P_1 It is also ovate in outline, being broader towards the centre of P_1 than in the opposite direction It is also slightly asymmetric, as the foliar buttress from which the next leaf will arise has begun to appear For the apex rises steeply from the base to the top of this buttress on the anodic side from P_1 and then becomes less steep, whereas on the kathodic side from P_1 it follows a more gradual curve as shown in figure $2D_1$

It cannot be said with certainty at which stage one plastochron ends and the next begins The elevation of the foliar buttress is no doubt part of a leaf-forming process, but whether the radial extension of the apex which precedes it is also associated with the formation of the next leaf is uncertain The convention will here be adopted of considering the start of a plastochron to be the first visible uprising of a new leaf, however small, but not of a foliar buttress

It has already been noted that P_1 is asymmetric, its kathodic flank being the longer The angle subtended by the smaller half of a leaf at the centre of the apex is a measure of the degree of asymmetry of the leaf In the normal plant the smaller half was always the anodic half, but this was not always so in the operated plants The arcs covered by the anodic half-leaves of normal plants were measured on the drawings, in the older leaves which had already formed tubes at their bases the meeting-point of these halves could only be recognized directly above the tubes.

A total of 46 angles were measured on 14 plants and the mean value was 166° 5 The extremes were 171° and 162°, the standard deviation was 2° 3, and the standard error was 0° 30 This asymmetry is also visible in the blade of the mature leaf of which the anodic half is usually slightly narrower than the kathodic The asymmetry of the leaves can often be seen not only in the length, or more strictly transverse extension, of the halves but also in their radial thickness, since the anodic half-leaf is often slightly thicker than the kathodic as can be seen in leaf 5, figure 1

To sum up, the asymmetry of the leaves is shown in the following features the anodic half-leaf is regularly the shorter in extension round the apex, and is also the outer in overlap in the upper parts of the leaf, in some leaves the anodic flank can also be seen to be the thicker radially, and at an early stage of development of P_1 it appears to be the more protuberant

Since the mean of an anodic half-leaf is 166° 5, and the mean divergence angle is only 152° 6, it follows that the centre of a new leaf is not directly over the meeting point of the flanks of the previous leaf, although that is the lowest point in the boundary line round the apex, but closer by 13° 9 to the centre of that leaf

THE EXPERIMENTS

(1) *Methods and terminology*

The operations were made under a Leitz Greenough microscope, usually at a magnification of × 75 In order to expose the apex it was necessary to split the sheaths of the older leaves and bend them back, but the younger leaves were too brittle to be bent back and had to be cut off a short way above their insertions By this means it was often possible to leave six or seven of the older leaves attached to the plant for photosynthesis As the plants bled strongly it was found best to leave them unwatered for at least 2 days before the operation When the operation had been made the apex was protected with cotton-wool until the bases of the cut-down leaves had grown up and covered it As the exposed apices were liable to be damaged by insects and mites, derris powder was applied to the bases of the cut-down leaves close round the apex This precaution did no harm and was usually, though not always, effective

The stage of the plastochron was recorded for each experiment at the time of operation The plastochron was divided into seven stages in terms of the size of P_1, the stages are given in table 1, p 140

After the operations the plants were left to grow for periods varying from 4 to 8 weeks, according to the temperatures The axillary buds grew out strongly and were continually removed, the removal of the young leaves being sufficient, as in other species, to cause them to grow out even when the stem apex was undamaged When the apices had grown enough they were pickled in spirit, embedded in collodion and sectioned by hand A few leaves present before the operation were included with the pickled apex

TABLE 1

size of P_1	arc covered by P_1, and its stage of development
very small	90°, just visible
small	90° to 180° (figure $2A_1$)
small-medium	over 180° (figure $2B_1$)
medium	nearly 360° (figure $2C_1$), hood arching over
medium-large	360°
large	hood further grown
very large	apex now extended in plane of P_1 and sometimes foliar buttress of I_1 visible

(2) *Preliminary observations on marked apices*

In order to test Hirmer's theory that a sector is inserted in the apex in such a way as to displace the centre of I_1, some preliminary marking experiments were made before the main experiments were undertaken Since the theory postulates that a sector of increased growth is inserted in the apex and displaces sideways a newly determined leaf centre, it follows that the tissues must be displaced at both sides of the inserted sector and also in the neighbouring regions * An attempt was therefore made to discover whether actually the tissues are so displaced Egg albumen mixed with charcoal was used for marking the apex It was applied with a single hair of a paint brush so as to form a fine streak across the apex and the cut-down bases of the youngest leaves, or else deposited in a straight row of dots If the streak became curved in the course of subsequent growth, or if any of the dots shifted so that they no longer formed a straight line, this was taken to indicate a displacement of the underlying tissues These observations were made under the dissecting microscope and recorded by free-hand drawings On Hirmer's theory the point at which the centre of I_1 is determined is displaced from a position opposite the centre of P_1 to the position which it occupies when I_1 becomes visible Since in *Rhoeo* the divergence angle is 152° 6 a displacement of 27° 4 should occur in the antidromic direction, that is, the opposite to that of the genetic spiral A streak or a row of dots extending across the apex along the diameter which passes through the centre of P_1 should therefore develop an antidromic curve in the region of the apex which is at 180° from the centre of P_1

In six of these experiments the streak or row of dots of egg albumen and charcoal lay either approximately along the diameter passing through the centre of P_1, or else along the closely neighbouring diameter passing through the meeting-point of the flanks of P_1 The latter diameter was sometimes preferred because the meeting-point of the flanks could be determined more accurately than the centre of P_1, and a displacement in the same direction along this diameter was to be expected Actually in three of the above experiments a slight antidromic displacement occurred in the part of the apex adjacent to the meeting-point of the flanks of P_1 This displacement was seen at the time when I_1 first became visible and was estimated at about 15°, but during the subsequent growth of

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* Hirmer (1922, pp 17, 18) and Troll (1937, vol 1, pp 421, 422) imply that their sectors of increased growth inserted in the apex expand more in one tangential direction than in the other But this is mechanically impossible, unless the neighbouring tissues of the apex offer more resistance on one side of each sector than on the other, which is not suggested by these authors, nor to be expected

I_1 a displacement in the opposite direction was noted, the line of marks tending to become straight again In two other experiments no displacement was seen near the meeting-point of the flanks of P_1 In the last experiment a slight *homodromic* displacement occurred in the part of the apex near the meeting-point of the flanks of P_1

In another five experiments the streak was placed in the plane at right angles to the median plane of P_1, or near it The ends of these streaks were farther from the position of Hirmer's supposed inserted sector, so that they would not be expected to be displaced so much by that sector, but some slight displacement might be expected Actually, of the ten portions of these five streaks which rested on the leaf-forming zone of the apex, nine remained straight until I_1 had arisen, and the tenth, which was between the centres of P_1 and I_1, was found to be slightly displaced towards the centre of I when I_1 had just arisen, in the opposite direction to that anticipated by Hirmer's theory

These results do not support Hirmer's theory For even in the three apices out of eleven in which the tissues were found to be displaced in the direction to be expected on that theory the displacements were not large enough, and in two others the displacement was in the opposite direction The marking experiments were therefore discontinued, and operations on the stem apex or youngest leaves were undertaken instead

(3) *The nature of the operations and classification of results*

Two kinds of operations were made on *Rhoeo* In the first the apex was split in a longitudinal median plane and the two halves were left to regenerate new apices The cuts were made through the median plane of P_1 or at right angles to that plane These operations were chosen as it was considered that splitting the apex would profoundly disturb the phyllotaxis system and that the positions of the first few leaves on the regenerated apices might provide evidence of the factors which determine the phyllotaxis of a normal plant The results of these operations suggested that in this species, contrary to what was found previously with *Lupinus albus* (Snow, M & R 1931, 1933 and 1947), the centres of the youngest leaves inhibit the formation of a new leaf centre, and that the intensity of this inhibition decreases with the age of the inhibiting leaf Accordingly, in order to test this hypothesis more directly, a second series of experiments was carried out in which the centre of P_1 was removed or destroyed at an early stage of the plastochron For on the hypothesis of inhibition a displacement of one or more of the subsequent leaves would be expected to follow, the inhibition due to the centre of P_1 having been removed, or at least reduced As the results of this second series of experiments were on the whole simpler and easier to interpret than those in which the apex was split, they alone will be described here and the others will be reserved for a later paper

In these experiments it was thought desirable to remove only the central part of P_1 leaving some portion of its flanks on the apex, as it seemed possible that if the whole visible part of P_1 were removed at an early stage in the plastochron the leaf might fail to develop at all, the amount of space available for I_1 would thereby be increased and any displacement of its centre might be attributed to this factor For this reason when the operation was made at a very early stage in the plastochron the central part of P_1 was first isolated by two cuts forming a V pointing towards the centre of the apex and the part of P_1 lying within the V was then removed The parts of the flanks lying outside the

TABLE 2 THE REMOVALS OF THE CENTRE OF P_1

DIVERGENCE ANGLES OF SUBSEQUENT LEAVES IN DEGREES

nos of experiments	size of P_1 at time of operation	angle P_2–I_1 (normal 305° 3)	deviation from normal (k=kathodic)	angle I_1–I_2	angle I_2–I_3	angle I_3–I_4	angle I_4–I_5	
	Group I, in which the centre of P_2 was left intact							
1	very small	285 5	19 8k	180 0	151 5	149 5	—	
2	small	305 0	0 3k	171 0	144 7	160 0	150 5	
3	small-medium	296 0	9 7k	185 3	140 0	—	—	
4	medium	294 5	10 8k	174 0	135 3	156 7	—	
5	medium	293 5	11 8k	179 3	122 0	—	—	
6	small-medium	289 0	16 3k	167 0	142 0	—	—	
7	small-medium	291 7	13 6k	196 0	113 0	172 0	148 0	
8	medium	279 5	25 8k	194 5	126 0	157 7	149 0	
	Group II, in which the centre of P_2 was also removed							
		angle P_3–I_1 (normal 457° 9)						
11	very small	457 0	0 9k	173 5	135 5	159 0	—	
12	large	—	—	187 4	139 0*	166 0*	154 0*	
	Group III, in which the centres of P_1 and P_2 were both removed but P_1 regenerated a new centre							
				angle P_1–I_1	angle I_1–I_2	angle I_2–I_3	angle I_3–I_4	angle I_4–I_5
9	very small	455 7	2 2k	185 3	170 0	131 0	157 3	143 0
10	very small	446 0	11 9k	181 7	167 0	135 0	157 0	—

Note All divergence angles are measured in the original direction of the genetic spiral except the last three angles marked with asterisks in no 12

TABLE 3 THE ASYMMETRY OF THE SUBSEQUENT LEAVES

ARCS COVERED BY THEIR ANODIC HALVES IN DEGREES

nos of experiments	I_1	I_2	I_3	I_4	I_5
		Group I			
1	183	177	180	—	—
2	176	172	180	167	—
3	170	174	167	—	—
4	178	171	175	—	—
5	180	170	175	—	—
6	171	172	168 5	—	—
7	202	170	180	—	—
8	200	158	168	161	171
		Group II			
11	—	170	178	174	—
12	—	164	190	175	170
		Group III			
9	170	173	173	169	—
10	175	176	174	170	—

Note In no 12 the measured halves of the leaves are those which are anodic in the new direction of the reversed genetic spiral

V were thus left on the apex When the operation was made at a later stage and P_1 subtended about 180° or more, its centre could be removed by a single tangential cut which still left parts of its flanks on the apex Finally in one experiment in which P_1 was very small the centre was destroyed by a puncture

In order to expose the apex it was unfortunately necessary to remove the hood of P_2 which arched over it The amount of P_2 which was removed varied considerably in different experiments Accordingly since there is reason to suppose that the central part of the base of P_2 affects the position in which I_1 will arise, four of the twelve experiments reported were excluded from the main group, since in them the central part of the base of P_2 was either severely damaged so that it possessed no median vascular strand or had been completely removed These four experiments are, however, included in tables 2 and 3, and will be described separately since they presented several points of interest In the eight experiments included in the main group, group I, P_2 had formed a basal sheath with a central vascular strand and in some had also formed a small blade, or two small blades, one from each flank In three of these eight the flanks of P_2 had been broken by the cut that had removed the centre of P_1, but the central part of P_2 was intact These eight experiments constituting group I will be described first

(4) *The development of P_1 when its centre was removed alone*

When the centre of P_1 was removed early in the plastochron while it subtended an arc of less than 360°, its flanks continued to extend round the apex until they met The other edges of the flanks of P_1 which abutted on the wound were found to have reunited at the base when the apices were sectioned The zone in which the two halves were united was low and did not usually reach above the level of the growing-point The manner in which the reunion took place is uncertain, as the material was not sectioned until after three or more weeks, but examination of the apex with the dissecting microscope a few days after the operation often revealed a strip of tissue beginning to grow up from the tissue of the apex immediately above the wound, that is, on the apical side of the wound It is thought that this strip of tissue, which will be called the 'reuniting zone', formed a bridge between the halves of P_1 It was usually narrow, showed the wound scar on its outer face and lacked a median vascular strand, as seen in figures 4 and 5, nos 6, 7 and 8 There was, however, one experiment, no 4, figure 3, in which the wound scar was seen on the inner face of the reuniting zone also Here it seems that this zone must have been formed from tissues internal to the wound and not from the undamaged tissue above it

Concerning the nature of this reuniting zone the most probable interpretation is considered to be that it was formed by an extension of the flanks towards the original centre of P_1 through tissue lying to the apical side of the wound or internally to it This possibility is supported by the fact that at a higher level each of the flanks usually formed a small and roughly symmetric blade, for this suggests that each flank had been partly reorganized to form a symmetric whole, though in the experiments of group I only one of these structures showed a thickened central region and enlarged median strand (experiment no 8, figure 5) The reorganization of the flanks was thus usually incomplete, but may have been sufficient to enable each flank to extend round the apex towards the original position of the centre of P_1 For such an extension, though in the abnormal direction relative to the centre of P_1, would have been away from the centre of the reorganized flanks, and so in the normal direction relative to those new centres Again in no 3, figure 4, the uniting zone was unusually thick radially and unusually high, it also had a median vascular strand and a large axillary bud In this experiment, therefore, it seems probable that the centre of

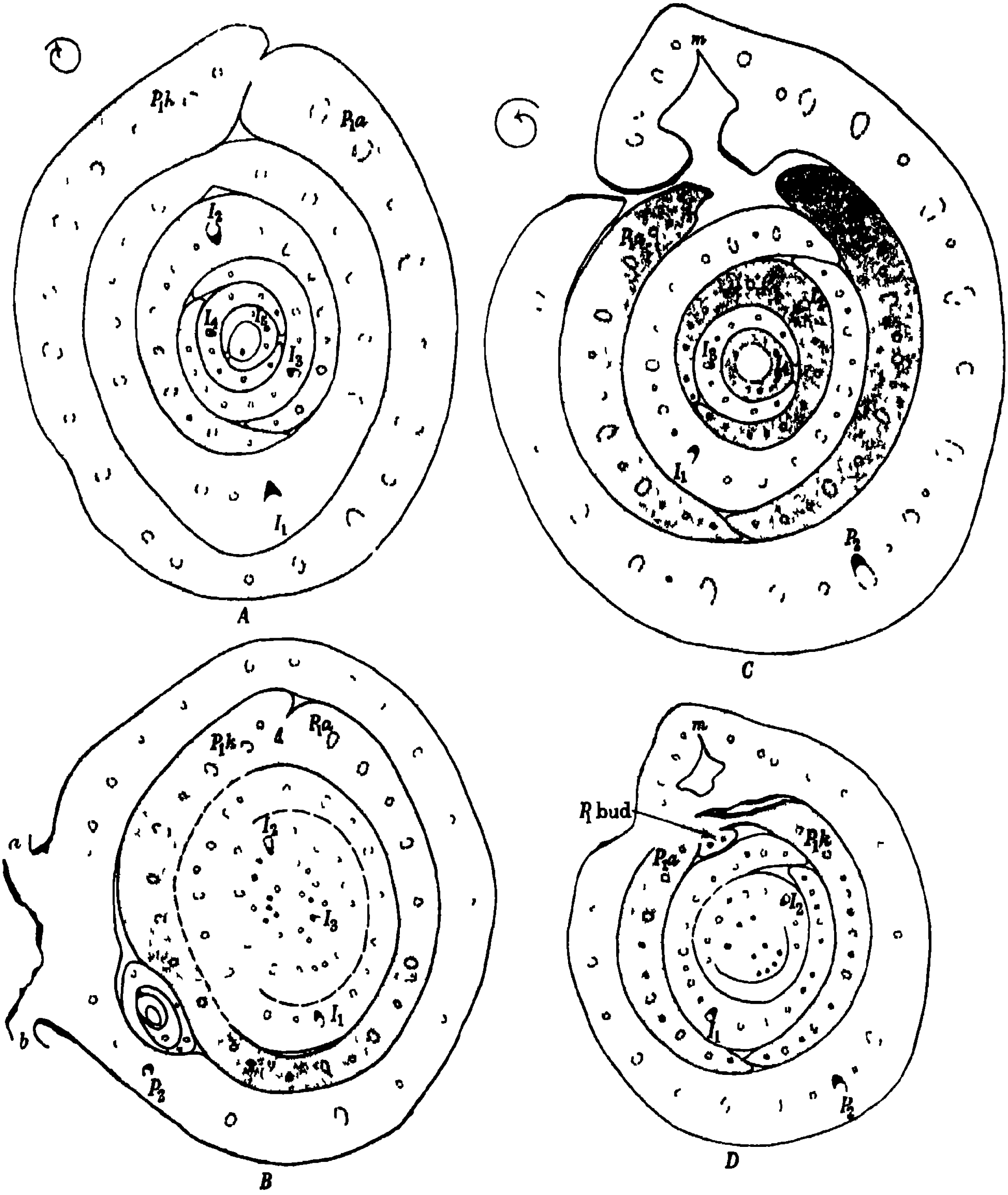

FIGURE 3 A and B are transections of no 2 from above downwards The centre of P_1 was destroyed by a prick In B, P_2 was united with P_3 at a and b C and D are transections of no 4 from above downwards The centre of P_1 was removed The flanks of P_2 have developed abnormally following injury In D, the central part of P_1 is joined to P_2 The meeting-point of the edges of the flanks of P_2 is marked m (Magn A and C, × 27, B and D, × 18) In this and subsequent drawings of experiments the wound scars are shown with a thick black line The spiral at the top left-hand side of each upper section shows the original direction of the genetic spiral P_1a and P_1k are the anodic and kathodic flanks of P_1 respectively P_1 and alternate leaves are stippled as also in subsequent figures

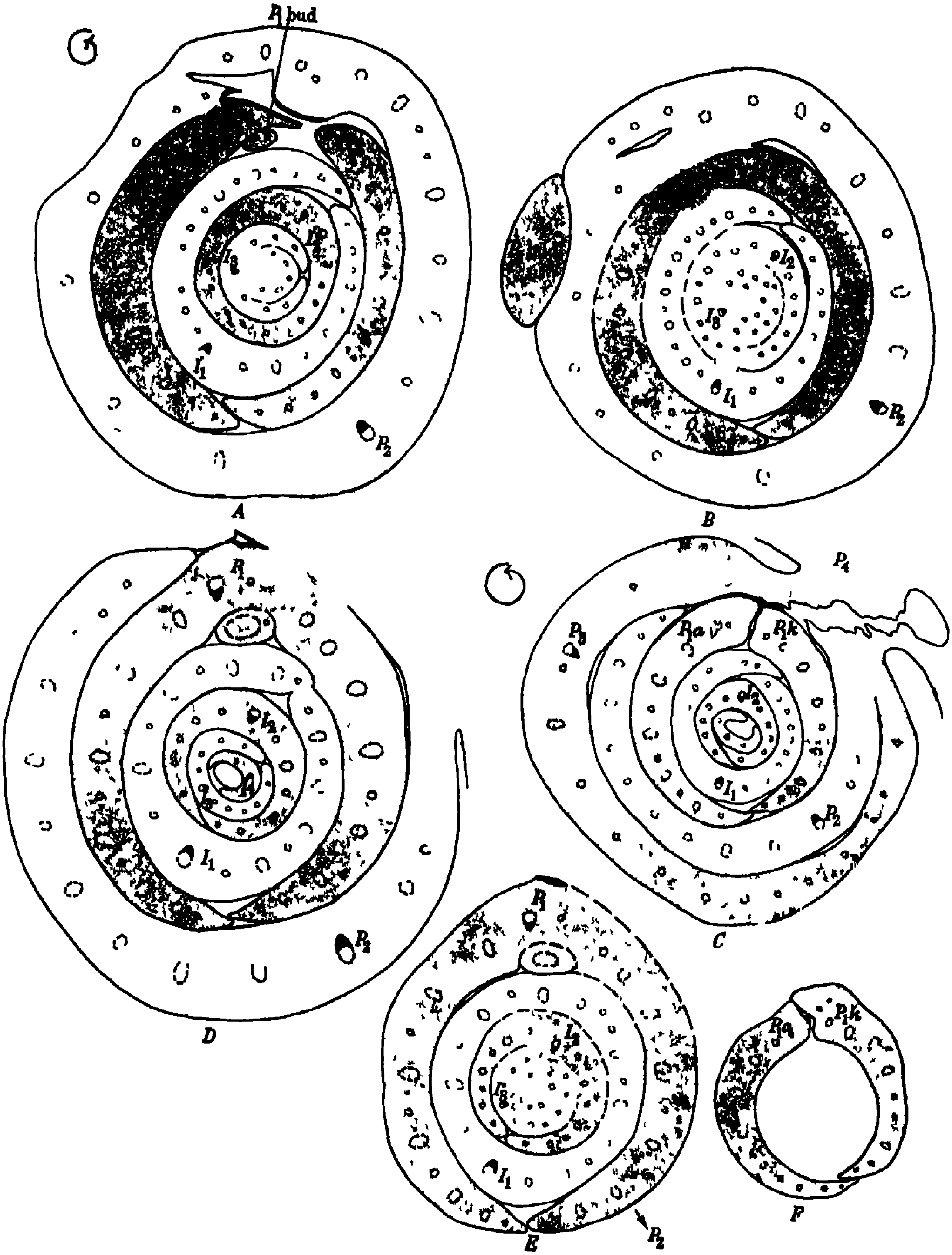

Figure 4 *A* and *B* are transections of no 6 at different levels The centre of P_1 was removed The central part of P_1 is joined to P_2 *C*, *D* and *E* are transections of no 3 at different levels The centre of P_1 was removed The adjacent faces of P_1, P_2, P_3 and P_4 were united on each side of a wound passing through them shown in *C* *F* is a transection of P_1 in no 3 at a higher level showing the leaf in two halves with no trace of a central vascular strand (Magn *A* and *D*, ×38, *B*, ×28, *C*, ×20, *E*, ×31, *F*, ×17)

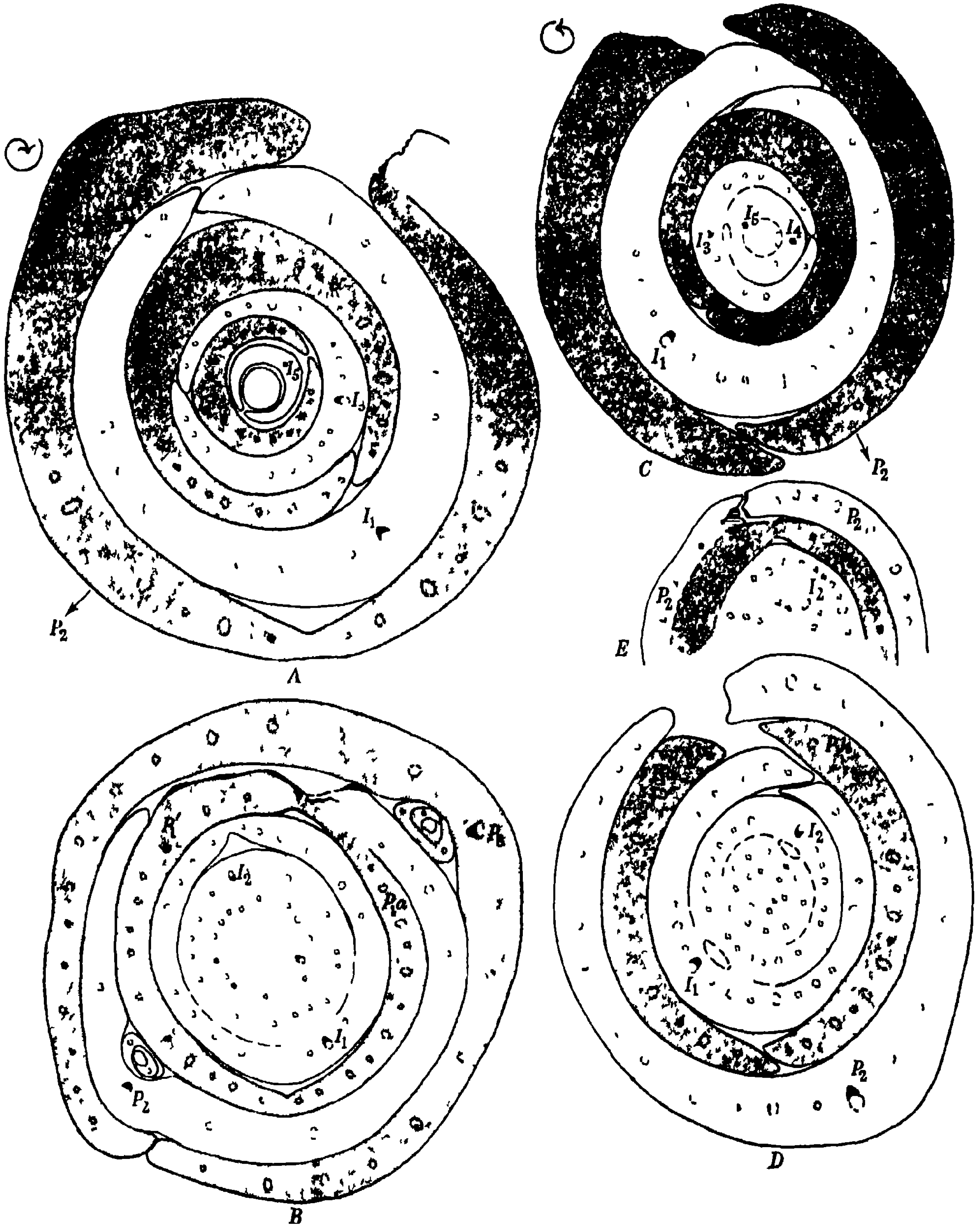

FIGURE 5 *A* and *B* are transections of no 8 from above downwards The centre of P_1 was removed. A new centre has probably been regenerated in the kathodic flank at P_1' The anodic flank has united with P_2 near the wound *C*, *D* and *E* are transections of no 7 from above downwards. The centre of P_1 was removed *E* is part of a transection showing the reuniting zone of P_1 just above its insertion (Magn *A*, ×28, *B* and *E*, ×15, *C*, ×31, *D*, ×22)

P_1 was not completely removed, the cut being either too shallow, or not reaching close enough to the apex so that the base of P_1 was able to grow up for a short distance This peculiarity of no 3 is significant for the interpretation of the subsequent phyllotaxis, as will be pointed out below

It needs to be mentioned that in several experiments, nos 3, 4, 6 and 8, the outer face of P_1 was joined to P_2 in the region of the wound, and in no 3, P_2 was in turn united with the older leaves These unions, which often occurred where deep wounds had been made, do not seem to have affected the subsequent phyllotaxis In four of these eight experiments an axillary bud had developed above the reuniting zone

(5) *The position of I_1*

In the eight experiments of group I in which P_1's centre was removed and the basal part of P_2 was intact, the position of I_1 was located by its angle from the centre of P_2, since its angle from the missing centre of P_1 could not be measured The mean normal angle from P_2 to I_1 in the direction of the genetic spiral may be taken as twice the mean of the single divergence angle already measured—that is 305° 5, and its standard deviation will be $0° 423 \times \surd 2 = 0° 6$

The divergence angles P_2I_1 of the experiments are given in table 2 They varied from 305° to 285° 5, with mean value 291° 8 The standard deviation was 7° 9, and the standard error was 2° 80 The experiments thus led to a decrease in the angle from the original position of the centre of P_1 to the centre of I_1 The difference between the mean angle of the normals and the experiments was 13° 5, and the standard deviation of the difference of the means was 2° 86 The difference may therefore be considered significant Examples of these experiments are shown in figures 3, 4 and 5, nos 2, 3, 4, 6, 7 and 8

This displacement of I_1 towards the missing centre of P_1 is to be expected if the centres of P_2 and P_1 act as centres of inhibition in determining the position of I_1 For the removal of the centre of P_1 would reduce the inhibition acting on I_1 from that direction, and consequently I_1 would be displaced towards the missing centre of P_1 by the inhibition from P_2 (see the diagram, figure 6) The variation of this displacement in different experiments may have been due to variations in the amount of the centre of P_1 that was removed and in the level to which the centre of P_2 was cut down There is little doubt that the experiments would have given more consistent results and showed a greater displacement of I_1 had it been possible to leave P_2 intact But this was impossible as already explained, since the hood of P_2 concealed P_1 and was too brittle to be bent back It is probable that the lack of displacement of I_1 in experiment no 2 was due to the injuries inflicted on P_2 at the time of operation (see figure 3*B*) For the central part of P_2 in experiment 2 was less thick than normal, but as its central vascular strand was present it was considered best to include the experiment in this group rather than with those experiments in which P_2's centre was removed completely, or so much of it that no central strand was present

It was thought probable that the displacement of I_1 would be greatest early in the plastochron, and that towards the end of the plastochron little or no displacement would occur, since the centre of I_1 would by then probably be determined, in its normal position For this reason all the operations but one were made fairly early in the plastochron, not later than the stage with P_1 medium Within this range from P_1 very small to P_1 medium the displacement of I_1 (column 4, table 2) shows no relation with the state of the plastochron (column 2, table 2) If any such correlation exists it has been obscured by other variable factors in these experiments It may be concluded that up to the stage with 'P_1 medium', I_1 is undetermined, since it can be displaced by an operation which does not touch its presumptive area The fact that the displacement does not exceed 25° in these experiments may be due in part to the cutting down of P_2 as suggested above, it is also possible that after the centre of P_1 was removed, some of its influence still persisted in the apex as a residual inhibition at the time when I_1 was determined

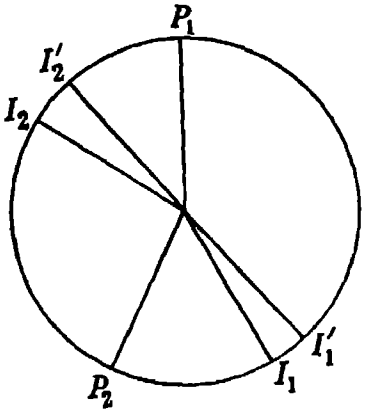

FIGURE 6 A diagram showing the changes in mean angular positions of I_1 and I_2 after the operations of group I The lines marked P_2, P_1, I_1 and I_2 show the normal angular positions of these leaves and those marked I_1', I_2' the mean angular positions after the operations

(6) *The position of I_2*

The position of I_2 must now be considered The angle I_1–I_2 is recorded in table 2 It varied from 167° to 196° measured in the original direction of the genetic spiral, the mean value being 181° 0 Since the normal divergence angle is 152° 6 with standard deviation 3° 7, it is clear that this angle is considerably greater than the normal The mean angles and the positions of I_1 and I_2 in the experiments and in a normal plant are shown diagrammatically in figure 6 This increase of angle would be expected on the inhibition theory, for the position of I_2 would be determined mainly by the inhibition from I_1, since the centre of P_1 had been removed and consequently P_1 did not inhibit I_2 at all strongly Any residual inhibition coming from P_2 would also tend to increase the angle I_1–I_2 (see figure 2) Thus the displacement of I_2 is to be explained as due mainly to the same cause as the displacement of I_1, that is, to the removal of the centre of P_1 and the consequent diminution of the inhibition from P_1 The variation of this displacement may also be related to variations in the inhibition from the remaining parts of P_1, and in the residual inhibition from P_2

In no 3 (figure 4 *C*, *D*, *E* and *F*) an unusually slight displacement of I_1 (9° 7) is associated with a large angle I_1–I_2 (185° 3) From this it would seem that the strength of the inhibition due to P_1 may have changed during the interval between the determination of I_1 and I_2, since otherwise a small displacement of I_1 would be expected to be associated with a relatively small angle I_1–I_2 This experiment has already been referred to (pp 143, 147) as one in which the uniting zone of P_1 was thick and showed a median vascular strand though the upper part of the leaf had made two separate blades, and this was thought to be due to an incomplete removal of the centre of P_1 which continued to grow for a short while after the operation If this explanation of the uniting zone is correct, it will also account for the unusual angles For if the centre of P_1 was still growing and exerting some of its inhibiting effect when I_1 was determined, only a slight displacement of I_1 towards P_1 would be expected, and if the centre of P_1 had ceased to grow when I_2 was determined, then it would not inhibit I_2, and so would not oppose the increase in the angle I_1–I_2

Actually the angle I_1–I_2 exceeded 180° in no 3, and in the two remaining experiments, nos 7 and 8, it was over 190°, it follows that in these three experiments I_1 was not the sole determining factor affecting the position of I_2 It is indeed possible that in no 7 the inhibition due to P_2 was greater than in the others, since it was noted at the time of pickling that in no 7 the central part of P_2 had grown strongly and had formed a small blade in spite of having been cut down at the time of operation In no 8 there is evidence that a new centre of P_1 had been regenerated in the kathodic half This new centre may have been partly responsible for the large angle I_1–I_2, for it can be seen from figure 5 that had I_2 arisen opposite I_1 it would have been extremely close above the new centre of P_1 In no 3 also it seems that P_2 must have exerted some influence, though less than in nos 7 and 8

(7) *The position of* I_3

Finally, the position of I_3 must be considered In all the experiments of the present group the centre of I_3 arose on the same side of the apex as in the normal plant, that is, on the side away from the centre of P_2 (compare figure 6), the angle I_2–I_3 being less than the normal (table 2) The genetic spiral thus continued in its original direction even in the three experiments in which the angle I_1–I_2 measured in that direction exceeded 180°, so that in these three I_3 arose in the smaller angle between I_1 and I_2 (nos 3, 7 and 8, figures 4 and 5) This result could not be explained on the inhibition hypothesis if I_1 and I_2 were the only leaves effective in determining the position of I_3 For were this so, I_3 should have occupied the larger angle between I_1 and I_2 in which the inhibition would have been less If, however, it is assumed that the residual inhibition due to P_2 was still effective when I_3 was determined, and that this inhibition was stronger than any that may have come from the remaining parts of P_1, then the position of I_3 in the smaller angle I_1–I_2 can be understood, since in these three experiments the smaller angle I_1–I_2 was on the side of the apex away from the centre of P_2

This assumption is supported by an experiment included in group II in which the centres of P_1 and P_2 were both removed (no 12, figure 8) In this experiment the angle I_1–I_2 was 187° 4 (table 2, column 5) and I_3 arose in the larger angle The genetic spiral was reversed and continued so This result seems especially important as it shows that the direction of the genetic spiral is not fixed in this plant but that it can be reversed by an operation comparatively remote from the apex, the removal of the centres of two visible leaves It also supports the suggestion that in this species a new leaf can be inhibited by a leaf four plastochrons older—P_2 in this experiment But this single result needs confirmation, and further experiments of this kind are therefore being done

The diminution of the angle I_2–I_3 can be understood as resulting from the increase of the angle I_1–I_2 For normally the centre of each new leaf partitions the larger angle between the two previous leaves, which is 360 − 152° = 208° (see figure 6) But in the experiments since the angle I_1–I_2 increased, the angle obtained by subtracting it from 360° decreased, and the centre of I_3 had to partition a smaller angle and so arose closer to I_2 than is normal The next few angles also, so far as they could be measured, oscillated above and below the mean normal angle, while tending to return towards it, except in no 1 (see table 2)

(8) *Four further experiments in which the centres of P_1 and P_2 were both removed*

The results of the four experiments forming groups II and III in which the centres of both P_1 and P_2 were removed are also recorded in table 2 The following points of interest may be noted The two experiments of group III, nos 9 and 10, figures 7 and 8, differ from those of group I not only in that the centre of P_2 was removed as well as that of P_1 but also in that P_1 appeared to have regenerated a new centre Thus in no 10 the kathodic flank of P_1 was considerably thicker than a normal flank in this region, and the vascular strand in the centre of this thickened zone was taken to be physiologically a new median strand But as there was no axillary bud above it, this is not certain Macroscopically P_1 was seen to have made two blades, of which the kathodic was considerably the larger and approximately symmetrical in the upper part

In no 9, figure 7, an entirely new leaf had been formed with its centre above the cut which had removed the centre of P_1 Since this leaf had no axillary bud, its median strand could not be identified with certainty, but it was taken to be the strand in the thickest part of the leaf marked P_1 in figure 7 Viewed macroscopically this new leaf had made an approximately symmetrical blade with a small kink at the top It is probable that the flanks of the original P_1 dedifferentiated after the centre had been removed, since no trace of them was found when the apex was sectioned This was the only experiment in which a single new leaf was regenerated after the centre of P_1 had been removed This regeneration may have been facilitated by two conditions first, P_1 was very young at the time of the operation, secondly, the centre of P_2 had been removed and its inhibiting influence on the formation of new leaf centres had consequently diminished

The position of I_1 in this group was located by its angle from P_3, since the original centres of P_1 and P_2 were lacking The normal angle P_3–I_1 may be taken as three times the mean normal divergence angle or 457° 9 The angles are recorded in table 2 In this group in which P_1 had regenerated a new centre, I_1 showed a kathodic displacement of 2° 2 in no 9 and 11° 9 in no 10, and its centre was approximately opposite to the supposed median strand of the new P_1 It therefore seems probable that the new centre of P_1 exerted a repulsive effect on I_1 This effect, however, cannot have lasted as long as in a normal leaf, since the centre of I_2 was close above the centre of P_1, the angle I_1–I_2 being 170° and 167° in the two experiments The fact that I_2 occupies the smaller angle P_1–I_1 in both these experiments raises the question whether any leaf other than the regenerated P_1 and I_1 was effective in determining I_2 It is suggested that P_3 was effective in doing so, since its centre lies on the same side of the apex as the larger angle between P_1 and I_1 (figure 7*B*, no 9) P_3 would thus play the same part in these experiments in determining I_2 as did P_2 in three experiments of group I (nos 3, 7 and 8) in determining I_3, for in both experiments a leaf arose in the smaller angle between the last two leaves, and the centre of a leaf four plastochrons older (P_2 or P_3) lay beneath the larger angle, while the centre of the leaf (P_1 or P_2) underlying the smaller angle had been removed As this situation occurred in five experiments it is not unreasonable to suppose that the centre of the leaf underlying the larger angle was effective as a centre of inhibition It is perhaps surprising that the centre of a leaf four plastochrons old should still inhibit effectively, but this question will be discussed later when the nature of the inhibition will be considered

The question may be raised how it was that in the experiments of this group P_3 did not inhibit I_1, which was, in fact, displaced towards P_3, although it has been concluded that P_3 did inhibit I_2 slightly From a cut-down leaf as old as P_3 only a slight degree of inhibition

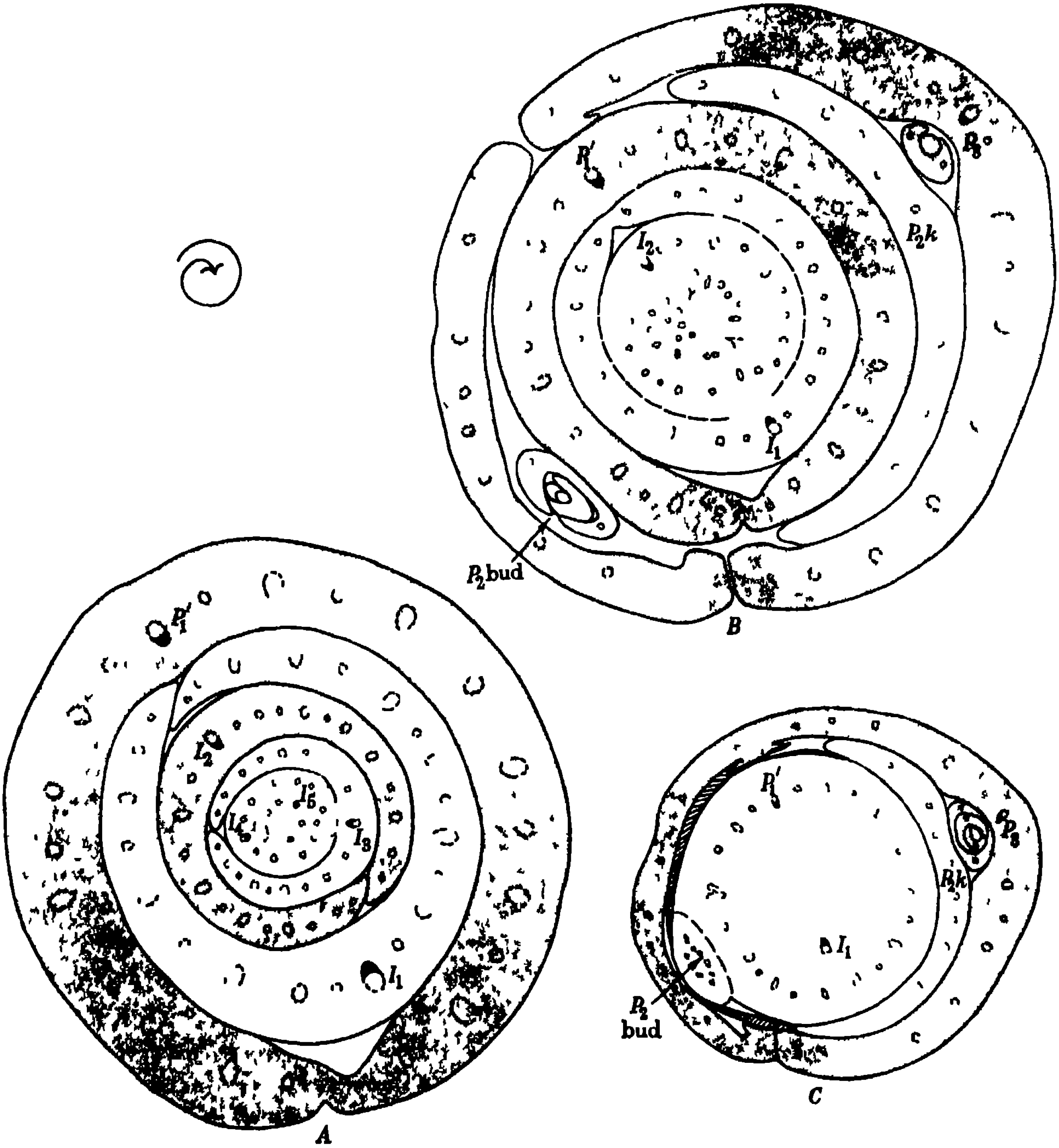

FIGURE 7 *A*, *B* and *C* are transections of no 9 from above downwards The centres of P_1 and P_2 were removed and P_1 regenerated a new centre at P_1' In *C* the vascular strands in the centre of the stem are omitted, the shaded area is the moribund base of P_2 and P_2k is its kathodic flank (Magn *A*, × 27, *B*, × 19, *C*, × 8)

would in any case be expected on the hypothesis adopted here This slight inhibition from P_3 acting upon I_1 may have been outweighed by an inhibition from the regenerated centre of P_1 acting upon I_1 in the opposite sense (see figures 7, 10)

Since I_2 arose in the smaller angle between P_1 and I_1 in the two experiments, the direction of the genetic spiral was unchanged, though the angle P_1–I_1 exceeded 180° measured in the original direction of the spiral The divergence angles tended to return towards the normal after oscillating above and below it

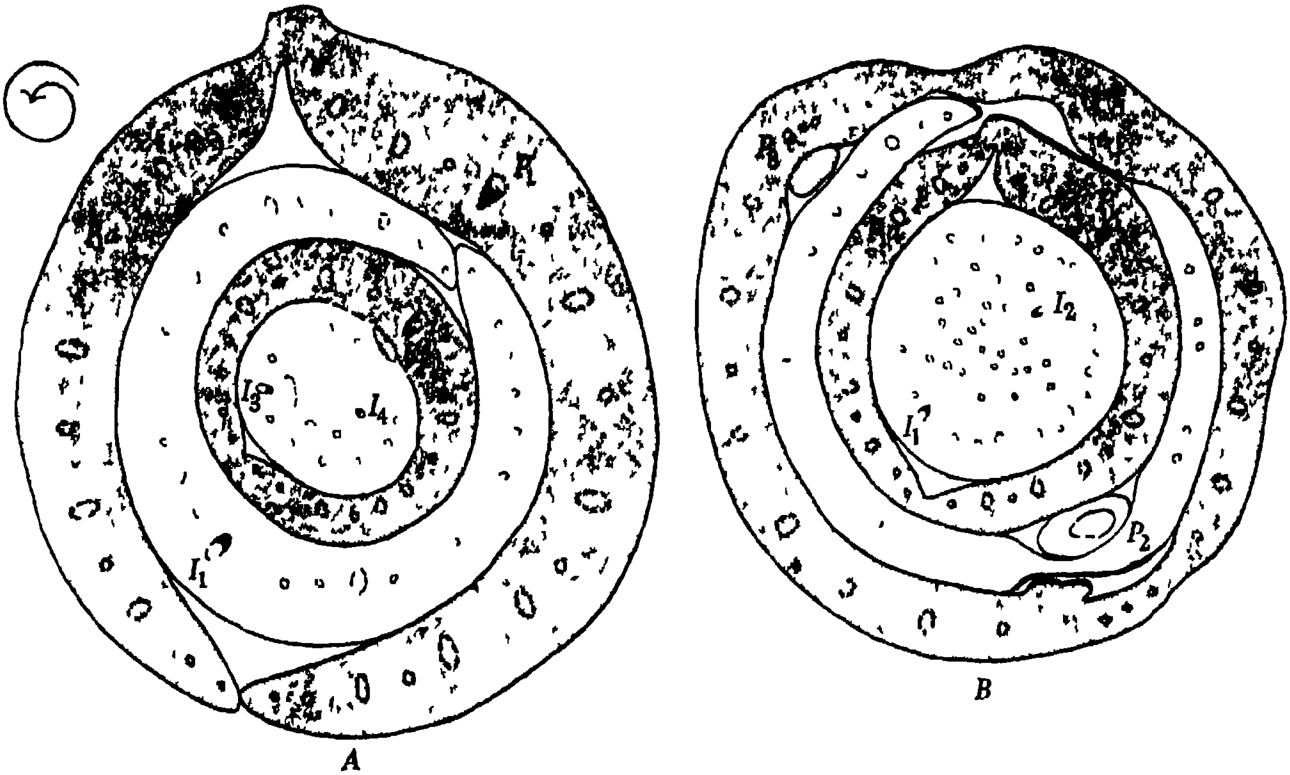

FIGURE 8 *A* and *B* are transections of no 10 from above downwards The centres of P_1 and of P_2 were removed A new centre was regenerated in the kathodic flank of P_1 at P_1' (Magn *A*, × 32, *B*, × 19)

There remain two experiments in which the centre of P_2 was removed, but P_1 did not regenerate a new centre—nos 11 and 12 In no 11 the angle P_3–I_1 differed from the mean normal angle by only 0° 9 The unchanged position of I_1 can be understood on the inhibition hypothesis, since on that hypothesis the inhibition from P_2 had been much reduced, so that it did not displace I_1 towards P_1 as it did in group I Whether this is a general rule will appear from further experiments now in progress In no 12, figure 9, the position of I_1 in relation to its normal position could not be ascertained, since the centre of P_3 had been accidentally destroyed The special interest of this experiment lies in the reversal of the spiral already mentioned on p 149 A further point worth noting is that it is the only experiment in which the centre of P_1 was removed late in the plastochron when P_1 was large The two halves of P_1 are united only at the base by a narrow strip of tissue which was dead at the time of pickling The tendency of the two halves to reunite was probably less strong than when the operation was made earlier in the plastochron The experiment of removing the centres both of P_1 and of P_2 is being repeated

(9) *The asymmetry of I_1, I_2 and I_3*

In the description of the normal apex it was noted that the leaves were regularly asymmetric, the anodic flank being the shorter in extension round the apex The mean angle subtended by the anodic half-leaf was 166° 5 The standard deviation was 2° 3 and the

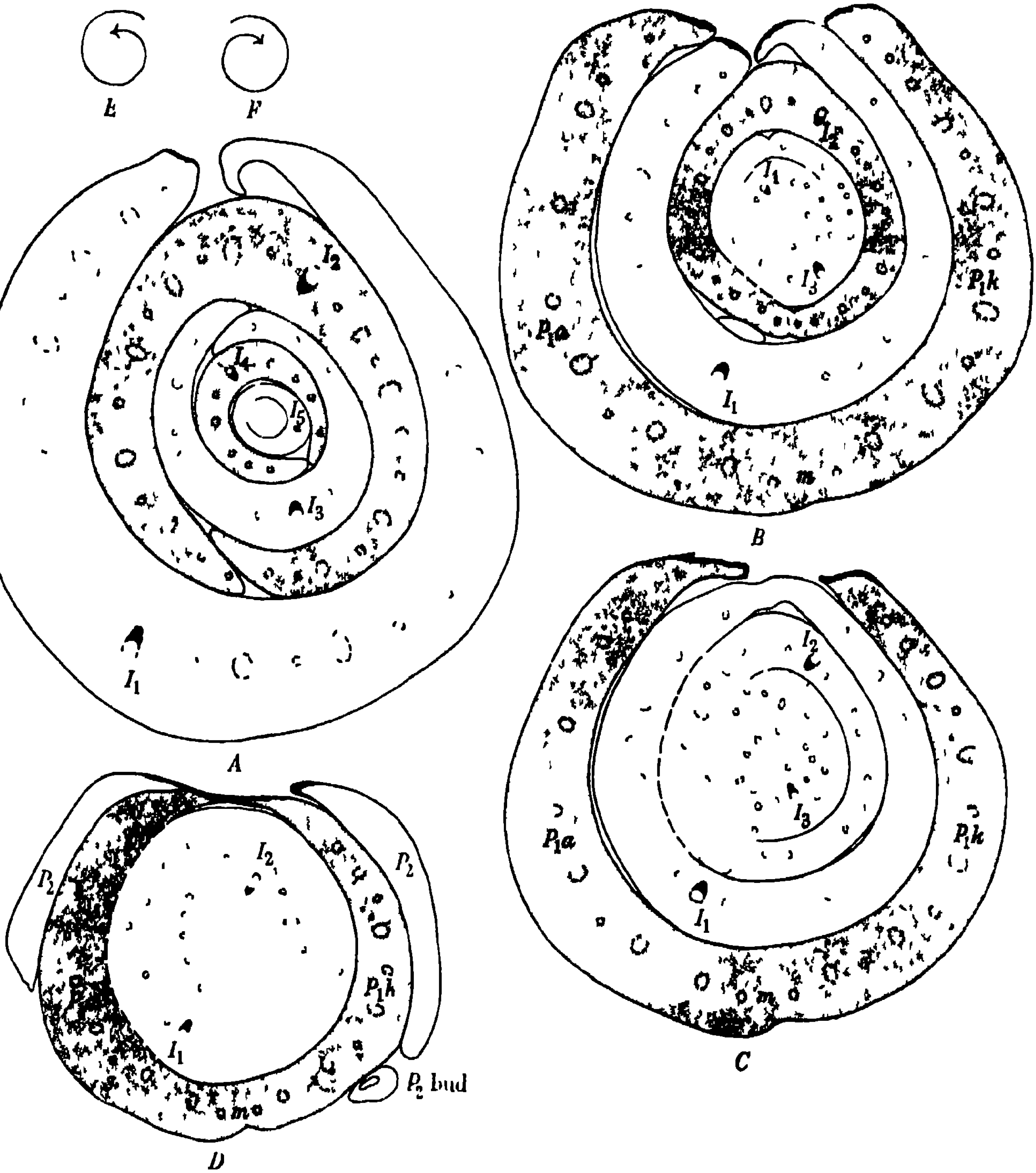

FIGURE 9 *A*, *B*, *C* and *D* are transections of no 12 from above downwards The centres of P_1 and P_2 were removed The meeting-point of the edges of the flanks of P_1 is marked *m* The vascular strands in the centre of the stem are omitted in *D* The sections shown in *B*, *C* and *D* are slightly oblique *E* shows the direction of the genetic spiral before the operation *F* shows its direction from I_1 onwards (Magn *A*, ×36, *B*, ×22, *C*, ×20, *D*, ×15)

standard error 0° 30 Though these experiments were designed to investigate the causes of the phyllotaxis, it seemed probable that they might also throw light on the factors determining leaf asymmetry, since in monocotyledons asymmetric leaves are usually associated with spirodistichous phyllotaxis and symmetric leaves with distichy Some relationship between the phyllotaxis and the symmetry of the leaves is therefore probable With this object in view the angles subtended by the anodic halves of the leaves that arose after the

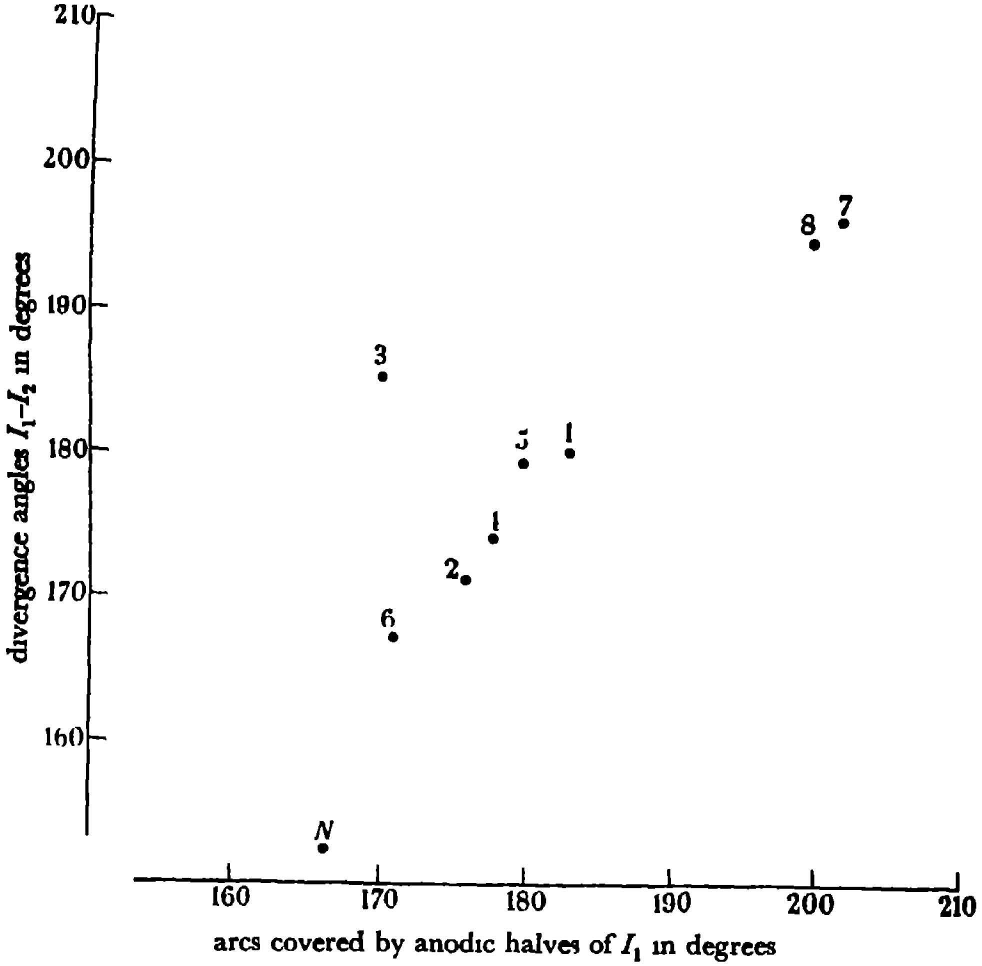

FIGURE 10 Graph showing relation between angle I_1-I_2 and anodic halves of I_1 in experiments 1 to 8 represented by numbered dots The dot N shows the relation between the normal means of the divergence angle and of the anodic half of a leaf

operation were measured and are recorded in table 3 The term anodic is here applied to the halves of the leaves which are anodic in the original direction of the genetic spiral except in no 12, in which the spiral was reversed at I_1, and the term anodic is applied in relation to the final direction of the genetic spiral

The angles subtended by the anodic halves of I_1 in the experiments of group I were always greater than normal They ranged from 170° to 202° This is interpreted as the result of a differential growth of the flanks For if the normal asymmetry of the leaf is due to the more rapid extension of the kathodic than the anodic flank, a differential change in their growth rates will bring about a corresponding change in their asymmetry Also if either flank is promoted relatively to the other it will extend farther round the apex before meeting the other flank and then will prevent it from extending any more For at their extreme base the flanks of each leaf meet and unite, as already mentioned (p 138), but do not overlap

The greatest increase in the anodic arc of I_1 occurred in nos 7 and 8, in which the angle I_1–I_2 also showed the greatest increase above the normal These facts suggested the possibility that there might be some regular relationship between the increase in length of the anodic halves of I_1 and the increase in the divergence angle I_1–I_2 This relationship is shown on a graph (figure 10) in which the angle I_1–I_2 is shown on the ordinates and the angle subtended by the anodic half of I_1 on the abscissae The graph shows clearly that the arc of the anodic half of I_1 increases as the angle I_1–I_2 increases except in no 3, in which the anodic half is unduly small This exception will be discussed below

The increase in the angle I_1–I_2 has already been explained as the result of the removal of the centre of P_1 and the consequent decrease in the repulsion exerted by that leaf on the centres of I_1 and I_2 Variations in this angle were considered to be due to variations in the amount of the centre of P_1 that was removed and in the degree to which P_2 was cut down (see p 148) Since the arc of the anodic half of I_1 varies directly with the angle I_1–I_2, there is reason to suppose that these same factors which caused the variations in the angle I_1–I_2 also caused those in the asymmetry of I_1

This provisional conclusion, together with some other facts to be mentioned below concerning the present experiments, and also some evidence from other experiments to be reported in a later paper, have led the writer to consider the following possibility with regard to the relationship between phyllotaxis and leaf asymmetry in this species, both in normal plants and in the experiments It may be that those conditions which *inhibit* the formation of a new leaf centre *promote* the extension of the flanks of a leaf round the apex A new leaf centre would then in general arise on the same side of the apex as the shorter half of the previous leaf, as is found to be the rule in a normal apex In terms of the inhibition theory it must be supposed that the influence exerted by the leaf centres on the subsequent leaves is such as to inhibit the formation of new leaf centres but to promote the extension of their flanks round the apex This hypothesis seems at first rather arbitrary and improbable, but it agrees well with the facts concerning the normal plant and concerning I_1 and I_2 in the experiments Thus in the experiments nos 1 to 8 which form group I the removal of the centre of P_1 reduced the promoting effect normally received by the kathodic flank of I_1, so that the anodic flank, as described above, was able to extend farther before meeting the kathodic flank

There remains to be considered experiment no 3, figure 4, which was an exception to the relationship shown by the graph, figure 10, in that the arc of the anodic half of I was considerably smaller in relation to the angle I_1–I_2 than in any other experiment of group I This arc was indeed only 170°, which is only 3° 5 greater than the normal arc, whereas the angle I_1–I_2 was over 180° Now in this experiment, though the angle I_1–I_2 is large, I_1 is only slightly displaced towards P_1, as was pointed out on p 148, where both these facts were interpreted as resulting from an incomplete removal of the centre of P_1 The same explanation may account for the slightness of the change in the asymmetry of I_1 For if the centre of P_1 was still growing when the flanks of I_1 were extending round the apex a relatively long kathodic and short anodic flank would be expected in I_1 as in a normal leaf

In nos 11 and 12 forming group II which are not included in the graph the asymmetry of I_1 could not be measured satisfactorily, since in no 12 the flanks of I_1 had grown into the wound which may have affected their relative growth rates (figure 9), while in no 11 the regeneration of the kathodic half of P_1 had interfered with the extension of the flanks of I_1 which did not meet round the apex These are the only two experiments in which there is definite evidence that developments near the wound had interfered with the flanks of I_1 In nos 9 and 10 forming group III the change in the asymmetry of I_1 was similar to that in the experiments of group I, though rather less than in most of them But it seems unprofitable to try to interpret the change in these two experiments, since the regeneration of a new centre of P_1, which probably took a considerable time, and the removal of P_2 made the conditions so complicated

The arc of the anodic half of I_2 also was longer than normal in the experiments of group I except in no 8 (table 3, column 3), in which it was shorter than normal In that experiment it seems that a new centre has been regenerated in the kathodic flank of P_1 (figures 5*A*, *B*), and this centre will, on the hypothesis proposed, have increased the extension of the kathodic half of I_2 above it, which in turn will have interfered with the extension of its anodic flank

In the remaining seven experiments of group I the increase in the anodic halves of I_2 may be related to the large angle I_1–I_2, for since I_1 and I_2 were more nearly opposite than in a normal plant the influence exerted by I_1 on the two flanks of I_2 was more nearly equal It may be noted that the longer flank of I_2 always lay on the opposite side of the apex from the centre of I_3, which agrees well with the hypothesis that conditions which inhibit the formation of a leaf centre promote the extension of the flanks round the apex

In no 12, an experiment of group II in which the centres of P_1 and of P_2 were removed, the asymmetry of I_2 is particularly significant In this experiment the genetic spiral was reversed permanently at the angle I_1–I_2 and the asymmetry of I_2 was also reversed, so that here again the longer flank of I_2 was on the opposite side of the apex from the centre of I_3

The asymmetry of I_3, however, is difficult to reconcile with the hypothesis proposed above which therefore remains for the present only a possibility to be borne in mind Since the asymmetry of I_3 is at present not understood it will not be described here, but the main facts are recorded in table 3 and in the figures

Discussion and conclusions

From the experiments on *Rhoeo discolor* reported above and from observations made on normal plants, information has been obtained with regard to three main questions These questions concern the manner in which a leaf primordium is determined and develops, the factors locating the position in which a primordium is determined and the causes of the asymmetry of the primordium They will now be discussed in turn

As to the first question the evidence indicates that in *Rhoeo* the centre of a primordium or a small central region is determined first and that from this centre the flanks extend round the apex until they meet For the fact that in *Rhoeo* the flanks of P_1 continued to extend round the apex after the centre of P_1 had been removed shows that once this extension has begun it does not depend on the presence of the centre It might, indeed, be suggested that the whole area occupied by P_1 had been determined to form a leaf before the centre was removed and was only gradually occupied by the flanks, but the results of some other experiments in which the apex was split do not support this suggestion In these experiments, which will be more fully reported later, the split was made at right angles to the median plane of P_1 When the operation was made early in the plastochron at a stage when P_1 subtended less than 180° the whole visible part of the leaf was confined to one of the split halves, and the flanks of P_1 did not develop on the other half, as they would have been expected to do if they had been already determined But they did continue to extend round the half-apex which carried the centre of P_1, extending through the tissue adjacent to the wound and above it On the other hand, when the split was made later in the plastochron so that the flanks of P_1 were severed by the cut, then the flanks continued to extend round the half-apex remote from the leaf centre, but not round the half carrying that centre The facts therefore indicate that the tips of the flanks of a leaf when once they are formed tend to extend round the apex or half-apex on which they are situated without needing any influence from the leaf centre for their further growth, and also that the flanks are determined later than the centre

Thus the manner of initiation and development of a primordium in *Rhoeo* appears to differ from that which was found in the dicotyledon *Lupinus albus* previously investigated For we concluded (1931, 1933) that in *L albus* a leaf primordium was determined as a whole as soon as a space was available both wide enough and low enough for it There was therefore a certain minimum area of the apex in which a primordium could be determined, and when a primordium was determined in it, this area constituted the primary area of the primordium (Snow, M & R 1933, p 360) This primary area included the stipules as well as the central part of the leaf, though some extension of the stipules round the apex was found to take place subsequently In *Rhoeo*, however, it appears that the primordium is not determined as a whole simultaneously but that its central part is determined first It is possible that some part of this central region constitutes a primary area, but if so it is much smaller in relation to the total area subsequently occupied by the leaf than it is in *Lupinus*

As to the factors locating the positions in which primordia are determined in *Rhoeo*, the present results indicate that each leaf centre inhibits the formation of new leaf centres in its neighbourhood and that this inhibition decreases with time and with distance The clearest evidence in favour of this conclusion is to be found in the positions of I_1 and I_2 following the removal of P_1, for the centre of I_1 then arose closer to the original position of the centre of P_1 than it would normally have done and I_2 arose almost opposite to I_1 These changes cannot be explained in terms of any space-occupying process, similar to that which we found in *Lupinus* For the centres of I_1 and I_2 usually did not fit into depressions in the changed boundary lines round the stem apices as can be seen in many of the figures, e g figs 3 *D* and 5 *D* Similarly, in a normal spirodistichous apex the leaf centres do not fit into any depressions, as was pointed out on p 139 Moreover, the displacement of I_2 after removal of the centre of P_1 indicates that in a normal apex of *Rhoeo* the position of a new leaf *n* is influenced by inhibition from leaf *n*–2, as well as leaf *n*–1 This inhibition from *n*–2 causes *n* to arise farther from *n*–2 than it would otherwise have done, and so causes *n* to deviate from the position opposite to the centre of *n*–1 in which it would otherwise have arisen on account of the inhibition from $n-1$ Consequently when the centre of $n-2$ is removed, leaf n arises more nearly opposite to $n-1$ This, then, as the writer concludes, is in the main the explanation of the spirodistichy of *Rhoeo*

There is evidence, however, that the position of the centre of leaf n is also affected by inhibitions from leaves $n-3$ and $n-4$ The inhibition from $n-3$ is shown when the angle I_1–I_2 exceeds 180°, indicating that I_2 is inhibited by P_2, which is $n-3$ in relation to I_2, and the inhibition from $n-4$ is shown by the position of I_3 which always arose on the side of the apex away from the centre of P_2, so long as that centre was intact, for this indicated that I_3 was inhibited by P_2 Thus $n-3$ reinforces $n-1$ and $n-4$ reinforces $n-2$ in their effects on n, as can be seen from figure 1 It may be that these inhibitions from $n-3$ and $n-4$ would not be found in all spirodistichous species, since they do not seem to be necessary for spirodistichy Other evidence was also reported for the conclusion that the position in which a leaf arises is determined by inhibitions from the four youngest leaves, their effectiveness diminishing with the age of the inhibiting leaf It is probable, however, that in a normal plant in which all these four leaves are intact the effect of the older leaves $n-3$ and $n-4$ is relatively less than it was in the experiments, in which the centres of $n-1$ and sometimes of $n-2$ had been removed

It is difficult to determine whether the diminution of inhibition with age of the inhibiting leaf depends for the most part directly on the age of that leaf, or on its distance from the apex which increases with age, but, since there is very little internodal extension between the youngest leaves, it is probable that the diminution cannot be accounted for by distance alone, but must in part depend directly on age

As to the mechanism of this inhibition, the experiments provide no direct evidence, but it seems probable that an inhibiting substance is formed by the centres of the leaves and diffuses through the tissues of the apex Whether it moves by simple diffusion or by some more complex process it is impossible to say, but is is clear that it must move upwards as well as transversely, since the four youngest leaves can all exert inhibitions on the new leaf arising at the apex The results indicate also that in *Rhoeo* the central region of a leaf is the main source of inhibition, since on that basis it has been found possible to explain them consistently They also suggest that the central conducting strand is the most effective part of that central region For in three experiments, nos 8, 9 and 10, in which P_1 regenerated a new central strand, the centre of I_1 was almost opposite to the new central strand, and so appeared to have been inhibited by the new strand But this inhibition seems to have faded sooner than that from a normal leaf centre, since I_2 arose with its centre close to the new central strand of P_1 This rapid fading may be correlated with the absence of a bud from the axil of the new centre of P_1, which seems accordingly to have been imperfect in some way On the other hand, the fact that in four other experiments, for instance, no 4, figure 3, a bud did arise in the axil of a P_1 with its centre removed, may be explained by its having been already determined

Finally, the problem of leaf asymmetry remains to be considered As stated in the introduction, Schumann at first considered leaf asymmetry to be the determining factor of the phyllotaxis, but later abandoned this view In Hirmer's opinion (1922) the asymmetry and the phyllotaxis both result from the insertion of a sector in the apex, but reasons have been given for considering it improbable that such a process takes place, and in any case it could not account for the fact that in *Rhoeo* the kathodic half (called by Hirmer 'anodic', see p 133) is the longer tangentially, contrary to what Hirmer states to be the general rule

Schoute (1913, pp 297, 310) considered that leaf asymmetry was secondary and occurred when the space available for a primordium was itself asymmetric provided that the new primordium made contact with the underlying leaves The new primordium then extended asymmetrically to fill the unequal gaps on each side of its centre This may, indeed, perhaps account for the fact that in *Rhoeo* the anodic half is usually slightly the thicker radially, since it lies above the meeting-point of the edges of the previous leaf, where there is the most space available in a radial direction, but it cannot account for the greater length of the kathodic half in normal plants The following results of the present experiments need also to be considered When the centre of P_1 was removed, the anodic half of I_1 increased in length and in three experiments exceeded the kathodic, and this increase varied directly with the divergence angle I_1–I_2, which also increased Again in no 9, figure 7, the centre of I_2 lay exactly over the meeting-point of the flanks of I_1, and yet I_2 was asymmetric, so that its asymmetry must have been due to something other than the space-filling process Lastly, in no 12, figure 9, in which the spiral reversed, I_2 was very asymmetric both in length of halves and in their radial thickness, and the longer flank was the thicker, contrary to what is found to be the rule in normal plants

The facts reported concerning I_1 and I_2 were shown to agree in the main with the hypothesis proposed, that the factors which inhibit the formation of a leaf centre promote the extension of a leaf flank round the apex, improbable though this may at first appear For in all the I_1 leaves except one, the longer flank lay on the side of the apex away from that on which the next leaf centre (I_2) was formed and thus on the more strongly inhibited side, as also it does in a normal plant The exception was no 3, in which it appeared that the centre of P_1 had been incompletely removed The most convincing evidence in favour of the hypothesis proposed is the correlation of the increases in the angle I_1–I_2 and in the arc of the anodic half of I_1 (see figure 10) The asymmetry of I_2 also was shown to support the hypothesis, but difficulties arose with regard to I_3 which cannot at present be resolved, so that the hypothesis must for the present remain provisional In other spirodistichous species the sense of the leaf asymmetry still needs to be determined with certainty

The differences between the processes of leaf determination in *Lupinus albus* and in *Rhoeo discolor* may now be briefly summarized as follows In *Lupinus* the primary area of a leaf is determined as a whole and comprises the greater part of the area of the apex which the leaf will finally occupy In *Rhoeo* the centre or a small central area is determined first, and the process of leaf formation extends gradually round the whole circumference of the apex In *Lupinus* the position in which the next leaf will arise depends on the position of the first space large enough to accommodate its primary area which reaches a sufficient distance from the growing-point, and so it depends on the outlines of the insertions of the youngest primordia In *Rhoeo* the position in which the next leaf centre will be formed depends on a balance between the physiological inhibitions exerted on the leaf-forming zone of the stem apex by the three or four youngest leaves

It does not appear that in *Rhoeo* the next leaf centre is determined in the position which is farthest from the growing-point, neither in the experiments nor in normal plants (p 139)

So in this respect also *Rhoeo* appears to differ from *Lupinus albus* and *Epilobium hirsutum*, in which species experiments led to the conclusion that the primary areas of leaves are determined in the available spaces that are lowest—that is, farthest from the growing-point (Snow, M & R 1931, 1933 and 1935) This is probably because in *Rhoeo* the physiological inhibitions proceeding from the young leaves may cause the lowest position to be unavailable for the next leaf centre Moreover, since the youngest leaf subtends an arc of 360° before the next leaf arises the boundary line round the base of the stem apex is much less indented than in plants with smaller leaf arcs, and the differences of level are therefore less great than in the latter

In view of the general similarity of the spirodistichous systems of monocotyledons, it seems probable that in the other species of monocotyledons with systems of this kind the process of leaf determination and the factors governing the positions of those leaves are similar to those in *Rhoeo* But this raises the question how it is that in the young seedlings of several spirodistichous species drawn by Hirmer (1922), though not in *Rhoeo*, several leaves following the cotyledon arise in a straight distichy, and then the later leaves deviate gradually into spirodistichy It may be that the inhibition from each of these early distichous leaves is weak and disappears before its second plastochron, so that the position of leaf *n* depends only on the inhibition from leaf *n*–1, opposite to which *n* arises Or again, it may be that these early leaves scarcely inhibit at all, and that their positions depend on a space-filling process such as we found in *Lupinus albus* For this process might be expected to place leaf *n* with its centre roughly over the meeting-point of the flanks of *n*–1, where the sheathing base of *n*–1 is thinnest, and since the distichous leaves are symmetric according to Hirmer, this position is opposite to the centre of *n*–1

Since the present results show that in *Rhoeo* the placing of new leaves is governed by physiological inhibitions from older leaves, they agree in this respect with the theories of Schoute (1913) and of Richards (1948) Yet those theories were not proposed especially for spirodistichous monocotyledons, but generally for all systems of phyllotaxis Indeed, it is mainly the much commoner spiral systems of dicotyledons which these authors have considered, and it was concluded previously (Snow, M & R 1931, p 36, 1933, p 396) that the results of experiments on *Lupinus albus*, a species with a typical Fibonacci spiral system, did not agree with Schoute's theory but needed to be explained in terms of space-occupying factors, in agreement with the theory of van Iterson The chief reason given for this was that according to Schoute a leaf centre is determined first, whereas the evidence from radial splits of I_1 in *Lupinus* was considered to show that in that species a leaf was determined as a whole (see Snow, M & R 1933, p 397) This conclusion has indeed been criticized by Richards (1948), but it would take too long to discuss here in detail these criticisms, with most of which the writer cannot agree It is hoped to discuss the question further when some further experiments now in progress are reported on leaf determination in dicotyledons

Even the results of the experiments on *Rhoeo* do not agree with the theory of Schoute, since he supposed that each leaf centre was surrounded by a 'dispersion area' within which an inhibiting hormone completely prevented the formation of other leaf centres, and that the effect of this hormone ceased suddenly at the boundary of each such area But it seems to the writer that the changes of leaf positions reported in *Rhoeo* cannot be explained on this basis, but only on the basis of inhibitions that decrease gradually with the distances from their sources

Wardlaw also (1949 *a*, *b*, *c*) has recently suggested a theory of leaf-determination and phyllotaxis in ferns according to which certain areas extending round the central parts of leaves already determined are made physiologically unavailable for the formation of other leaves, and he has based this theory on some valuable experiments on fern apices, which, however, are morphologically different from those of flowering plants

The theory of Richards (1948) is much less rigid than that of Schoute, and is stated only in very general terms Unlike Schoute he supposes that the inhibiting influences from existing leaves diminish continuously with distance He claims that on theories such as his own, which he calls field theories, it is possible to explain the return of a spiral system to regularity after a disturbance This is a very important claim, since the return to regularity after a disturbance and the attainment of regularity in seedlings are serious difficulties for a space-occupying theory such as that of van Iterson

The present experiments on *Rhoeo* support very well Richards's idea of inhibitions diminishing continuously with distance, and they contain nothing contrary to his theory Yet difficulties arise for this theory also if it is applied to dicotyledons, since Richards, like Schoute, supposes that the centre of a leaf, or at most a small central area, is determined first, whereas the evidence, as has been pointed out, still seems to the writer to show that in *Lupinus* a leaf is determined as a whole Another difficulty is that on the theory of Richards the position of a new leaf should depend on inhibitions coming from all the leaves of the uppermost cycle at least Yet in *Lupinus* the evidence has seemed to show that the position of a new leaf *n* does not depend, or not appreciably, on the immediately previous leaf *n*–1, when leaf *n* does not make contact with that leaf, as normally it scarcely does The position of *n* depends only on those leaves with which it does make effective contact The evidence for this statement was summarized recently (Snow, M & R 1947, pp 14, 15, 1948, pp 271, 272) in a criticism of the so-called repulsion theories of phyllotaxis, and it seems to the writer to hold good in spite of criticisms made in correspondence by Richards Further experiments bearing on this point are also in progress

A similar conclusion has been reached by Wardlaw (1949*a*, pp 173, 188, 1949*c*, pp 106, 125) from experiments on fern apices In these apices the visible leaves are not in contact at all, but Wardlaw has concluded that here also the position of a new leaf is affected only by the immediately adjacent leaves, and not by those remote from it (1949*a*, p 188) These fern apices having five leaves in the top cycle are very well suited for testing this point He has also written that the position of a new leaf is determined by localized factors and not by factors affecting the meristem as a whole (1949 *a*, p 177)

The writer concludes therefore that the process by which leaves are localized in spirodistichous monocotyledons is different from what it is in dicotyledons and ferns, and that the phyllotaxis of the first of these groups depends on physiological inhibitions such as are postulated by Richards, but that his theory cannot hold good for the other two groups, or not in its present form at least The problem for the future seems to be whether in dealing with the dicotyledons and ferns it is possible in any way to secure the advantages claimed for the theory of Richards without coming into conflict with the experimental results

I should like to thank Dr C D Darlington, of the John Innes Horticultural Institute, and Dr H Gilbert Carter of the Botanic Garden, Cambridge, for kindly supplying cuttings of *Rhoeo discolor*, the directors of Botanic Gardens of Ghent and Utrecht for sending seeds, Mr G W Robinson, of the Botanic Garden, Oxford, for raising the seedlings and cuttings, and lastly my husband, who first drew my attention to the problem of spirodistichy, for help during the course of the work and in presenting the results

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THE MIGRATION OF THE DESERT LOCUST (*SCHISTOCERCA GREGARIA* FORSK.)

I. THE BEHAVIOUR OF SWARMS

II. A THEORY OF LONG-RANGE MIGRATIONS

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(*Communicated by V. B. Wigglesworth, F.R.S.—Received* 17 *May* 1950)

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Vol. 235. B. 625. (Price 30s.) 22 [Published 31 May 1951

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PART I THE BEHAVIOUR OF SWARMS

SUMMARY

New evidence is given on the behaviour of migrating Desert Locust swarms, based upon some sixty encounters by various observers with swarms in Iran in 1943 and in Kenya in 1944 After describing the process by which a swarm launches on migration in the morning, the observations are used to illustrate the separate influence of locust condition, wind, gregariousness, the sun and landscape on the behaviour of swarms

Migratory activity increased gradually after the last moult, but the tendency to fly reached full development when hardening of the cuticle was still not quite complete, whereas flight vigour, as shown by the ability to resist carriage by the wind, did not reach full development till later Migratory activity became reduced again around the time of mating and egg laying but continued until death Special attention was devoted to behaviour in relation to wind, with recording of wind speed and height of flight as well as wind direction and the courses and tracks of the flying locusts Close, continuous observations of single swarms and the numerical data accumulated suggested that low fliers tend to stabilize their ground speed by varying their air speed according to the wind speed, and showed that they tend to come down and even settle when the wind is too strong for them to make headway against it, to take off and rise in the air when the wind speed is lower, to orient into the wind as long as they can make headway but to turn aside and commonly to turn right round and fly with the wind when they can no longer make headway and do not settle Rather higher fliers behaved in a parallel manner, but were distinctly less responsive to wind changes than lower fliers When parts of the same swarm were observed over land and over water, the latter failed to respond to wind changes when the former did so Mutual stimulation among swarm members was observed to reinforce flight activity, to make the locusts keep together and fly in parallel, thereby stabilizing the direction of the swarm as a whole (*gregarious inertia*), and to accelerate mass changes of direction initiated by external agencies such as wind There was no consistent relation between the direction of the sun's rays and the locusts' orientation, but there was evidently some direction-stabilizing agency at work other than gregarious inertia, and reasons are given for supposing this to be a light-compass-reaction to the sun Evidence was obtained that the avoidance of upstanding obstacles is merely a special case of a general effect, a 'compensatory' change of direction being caused by any gross movement across the eyes This type of optomotor reaction is regarded as contributing to the observed tendency to fly along lanes, through trees, along shore-lines and valleys

There follows a critical review and further analysis of the foregoing and previously published observations, temperature and moisture being considered as well as the influences already mentioned The extremely confused picture presented by the data accumulated hitherto on flight direction in relation to wind direction, is attributed to a tendency to seek some universal relationship, without sufficient regard to the varying circumstances at the time of observation, especially the wind speed and the height of flight When these are taken into account, there are indications of a regular system of relations between flight direction and wind direction The wind appears to be a most important direction-determining agency which acts, not only by carrying the insects, but through the optomotor reactions of the insects to the apparent movement of the visible substrate Migratory flight occurs as the normal, 'spontaneous' activity of gregarious locusts when at or near their preferred temperature The suddenness of the *mass departure* of a swarm in the morning is attributed primarily to gregariousness As flight activity increases with rising temperature, mutual stimulation among the locusts also increases and finally transforms the disorderly mob of insects into a coherent swarm, for the first time able, and now obliged to move off *en bloc*

Finally, all the available information is used in an attempt to distinguish what aspects of its behaviour are peculiar to the migrant locust, hopper or adult, and to find their underlying cause The primary characteristic of the migrant is its locomotion, which is carried on with extraordinary persistency through each day and day after day, while other forms of activity are relegated for the time being to a quite subsidiary role The tendency to go straight has often been regarded as an equally fundamental characteristic of large insect migrants, but it appears rather to be secondary, an outcome of the locomotory 'drive' Locust migrants have no 'goal' and no special 'directional sense' Their orientations are governed not by any single one but by a number of reactions, mainly of the optomotor type, to fellow-individuals, the sun, the wind and to other gross features of their ever-changing environment What is peculiar about the migrant in this connexion is the unfamiliar *pattern* in which familiar reactions are arranged, resulting in some changes of direction, but also in an unusual amount of moving steadily in one direction This peculiar pattern seems to be due to the combination of the migrant's peculiar neuro-physiological state in which reactions to stimuli which would arrest it are suppressed, with the peculiar pattern of its sensory experience during continuous locomotion Thus external features which are the most constant concomitants of the moving insect, such as wind and sun and fellow-locusts, become especially effective as sources of stimulation when their relation to the insect is changed by them or by it, its reactions to them having thus a certain stabilizing influence on its direction The migrant's tendency to stabilize its sensory relations with the environment is shared by non-migrating insects, and is no more peculiar to the migrant than are the types of regulatory reaction employed It is concluded that the key to locust migratory behaviour, in all its aspects, is the opposition between two powerful tendencies of the insect the tendency to locomotion and the tendency to sensory regulation Keeping on a straight course is merely one of the ways in which this conflict is resolved

(See p 261 for summary of Part II)

INTRODUCTION

The Middle East Anti-Locust Unit was formed by the Colonial Office in 1942 to organize, under the technical supervision of the Anti-Locust Research Centre directed by Dr B P Uvarov, control measures against the Desert Locust plague that had started in 1939–40 (see Uvarov 1943) As a member of this Unit during 1942–44 my particular task was to develop the use of aircraft for dusting adult locusts with contact poisons (see Gunn 1948*a*) The study of behaviour was envisaged as a central part of the work, since the mobility of swarms is a principal obstacle to successful attacks upon them The observations were inadequate to solve the behaviour problem then thought to be of most immediate importance for successful attack from the air, namely, what determines the time a swarm remains at its night roosting site before flying away in the morning This problem was taken up by a subsequent expedition (Gunn, Perry, Seymour, Telford, Wright & Yeo 1948) But the observations threw some light on other aspects of Desert Locust migration, particularly the effects of wind and of the phase of the insects

The material on hopper migration obtained during the same period was put together soon afterwards (Kennedy 1945), mainly as a starting point for consideration of the material on adults now presented here There was more material on adults and it was more difficult to analyze, especially so since the literature on the subject is very extensive and general principles are only beginning to take shape However, the painstaking collation and analysis of innumerable locust reports by the Anti-Locust Research Centre in London (notably Waloff 1946*a*), the work of Rao (1942) and his staff in India, of Predtechensky

(1935*a*, 1935*b*) in the Middle East and Central Asia and of Zolotarevsky and his staff, and of Volkonsky (1942) in north-west Africa, have recently added so much to our knowledge of Desert Locust migrations that a new phase in its development can be said to have opened Although much remains to be clarified concerning locust migration, it is already better understood than the familiar examples of migration in other insects, excepting only the army ants (*Eciton* spp) (Schneirla 1940, 1945, 1949 and other papers cited therein)

The present work is not an attempt to review the whole subject Its object is rather to contribute to the framework of general ideas which must be constructed before a final synthesis will be possible The work is divided into three parts This part, part I, is an analysis of the migratory behaviour of fully swarming locusts based on direct observations of them New observations are quoted separately first, followed by a discussion of certain influences affecting migratory behaviour in the light of both the field observations and the relevant literature In conclusion, the behaviour of gregarious locust migrants, both adults and hoppers, is considered as a whole in an attempt to identify what is distinctive about it Part II utilizes the observations and deductions of part I for the elaboration of a theory of long-range migrations, which are considered to be a problem in themselves Part III (Kennedy, in preparation) quotes some original observations on migration among non-swarming locusts and then discusses them, together with other evidence from the literature, in an appraisal of the relation between the phase of the locusts and the manner and results of their migration

The field assistance of the following workers is most gratefully acknowledged Messrs H S Darling, A G Hussain, Taqi Ahsan, O B Lean and Professor A N Scherbinovsky (in Iran), and Leading Aircraftsman Hill and other members of the Anti-Locust Flight, Middle East, R A F (in Kenya) If those in the Middle East Supply Centre and elsewhere whose administrative assistance, given in distracting war circumstances, made the work possible, are not mentioned by name, it is only because the list would be so long Needless to say it is to Dr B P Uvarov that the principal acknowledgement is due, not only for originating the expeditions during which the field work was done and for supplying additional data, abstracts and translations from the files of the Anti-Locust Research Centre, considerable clerical assistance, etc , but most of all for stimulating discussions During the years since 1944 in which this work has been in preparation I have had the benefit of much discussion with him, with my friend Dr D L Gunn and with Miss Z Waloff of that Centre Where any credit is due, they must share it It should be understood, however, that the theories and conclusions put forward are not agreed upon and I alone take responsibility for them

OBSERVATIONS

Locusts observed

Table 1 sets out the dates, places and types of the swarm observations to be described. A more particularized list, excluding observations on 'fledgling' and mating swarms and on swarms seen over Lake Naivasha on 23 to 24 May 1944, is given in Table 2, where the observers are also indicated Cases not observed by the writer himself have been included only when it was possible to question the observer directly, and most of these observers were themselves locust specialists

The observations fall into two main groups (i) on swarms of two successive generations in the course of the spring–summer, 1943, generally northward migration through Iran (refs 5 to 38), and (ii) on swarms of two successive generations in the course of the spring, 1944, generally northward migration through the Rift Valley Province of Kenya (refs 39 to 53)

Small samples of the locusts observed in south Iran were collected and their elytra and femora measured on the spot Their E/F ratios are tabulated as frequency distributions in table 3

TABLE 1 PLACES AND DATES OF OBSERVATIONS ON SWARMS OF DIFFERENT TYPES

				swarms observed					
				semi-migrants		full migrants			
						pink		yellow	
country	district	month and year	generation	fledglings	mating and ovipositing	no	ref	no	ref
Arabia	Oman and Dhufar	xii /42	monsoon and winter	—	—	4	1–4	—	—
Arabia	Oman and Dhufar	iv /43	first spring	—	—	1	5	—	—
Iran	Jask	iv /43	first spring	—	—	5	6–10	—	—
Iran	Bandar Abbas-Hajiabad	iv /43	first spring	—	—	5	11–15	3	16–18
Iran	Kerman-Anar-Rayin	v–vi /43	first spring	—	4	1	19	10	20–28, 30
Arabia	Riyadh	v /43	second spring	—	—	1	29	—	—
Iran	Bam	vi /43	second spring	4	—	6	31–36	—	—
Iran	Birjand	vii /43	second spring	1	—	2	37–38	—	—
Kenya	Naivasha-Nakuru	iii–iv /44	short rains	—	1	6	39–44	7	45–51
Kenya	Naivasha-Nakuru	v /44	long rains	—	—	2	52–53	—	—
			totals	5	5	33	—	20	—
				10		53			

Locusts, apparently belonging to two successive generations, had been observed moving effectively northwards through Oman (east Arabia) at the end of 1942 Refs 1 to 4 in table 2 cover the only dense, fully migrant swarms observed at this time The loose formation and non-persistent manner in which most of them flew led to the conclusion that these locusts were not fully *gregaria* even in behaviour An account of the observations made on them is therefore left for part III However, the younger Oman locusts belonged to the generation which was held partly responsible for the winter, 1942–3, invasion of south Iran Breeding occurred in Oman and south Iran on the winter rains, and the Bandar Abbas (south Iran coast), April 1943, sample (table 3) was taken from the new, first spring generation, at a time when these locusts had become sexually mature in their turn They behaved like fully *gregaria* swarms, although some of them had E/F ratios that Rao (1942) would class as *congregans* or even *solitaria*

The sample of yellow, mating locusts taken in late May 1943, from a swarm at Anar, 450 km inland from Bandar Abbas, were more nearly *gregaria* biometrically and in appearance, although probably belonging to the same generation as the young Oman and Bandar Abbas samples All the other locusts observed—that is, in swarms of the first spring generation in the Kerman-Anar-Rayin district (central south Iran) in May–June 1943, of the second spring generation in east Iran in June–July 1943, and of the short-rains and long-

TABLE 2 PARTICULARIZED LIST OF OBSERVATIONS ON MIGRANT SWARMS

ref no	date	time (local)	place	obs.	wind		locusts					remarks
					direction to	speed (m./sec.)	colour	height (m.)	track	swarm size	density	
1	19 xi 42	1300	Muscat	LI	NW	1	grey and pink	10–200	C	medium	loose	—
2	21 xi. 42	1800	Masirah I	LI	S	1	grey and pink	0–30	N	medium	loose	many settled
3	25 xi 42	1300	Salala	LI	?	1	grey and pink	0–100	C	medium	dense	many settled
4	21 xii 42	1200	Dibai	JSK	SW	3	grey and pink	0–10	NE	very small	loose	many settled
5	8 iv 43	1500	Ras al Khaima	DVF	E	1	pink	0–10	W	small	loose	part settling
6–10	13–17 iv 43	all day	Jask	AGH	E	17	pink	0–100	E	large	loose	succession of flights
11	25 iv 43	1800	Guhra	OBL	—	nil	pink	0–10	NW	large	loose	part settling
12	26 iv 43	0900	Kutawad	OBL	—	nil	pink	0–100	NW	large	loose	part settling
13	26 iv 43	1200	Gakum	OBL	—	nil	pink	30–300	W	large	loose	part settling
14	27 iv 43	0800	Ab-i-Din	ANS	SW	1	pink-yellow	10–100	NE	large	loose	part settling
15	27 iv 43	1400	Hajiabad	TA	—	nil	pink-yellow	50–200	C	small	scattered	—
16	30 iv 43	1400	Sirjan	OBL	E	1	yellow	0–10	N	medium	loose	part settling
17	30 iv 43	1500	Chashmeh Sefid	OBL	SE	1	yellow	5–15	SE	small	loose	—
18	30 iv 43	1600	Ahabad	OBL	SE	2	yellow	5–20	NW	very small	scattered	—
19	1 v 43	1100	Guhra	OBL	SE	1	pink	0–10	W	small	loose	part settled
20	20 v 43	10–1100	Kerman	JSK	SE	1–3	yellow	0–200	NW	medium	loose	succession of flights
21	20 v 43	1200	Baghin	JSK	SE	1–3	yellow	0–200	NW	small	loose	succession of flights
22	20 v 43	1500	Kabutar Khan	JSK	S	2–5	yellow	0–10	NW	medium	loose	succession of flights
23	21 v 43	1000	Bayaz	JSK	SE	3	yellow	0–10	NW	medium	loose	succession of flights
24	21 v 43	1100	Sherifabad	LI	S	7	yellow	10–100	S	medium	loose	down-wind short period only
25	21 v 43	1500	Kabutar Khan	LI	SE	7	yellow	0–10	SE	medium	loose	down-wind short period only
26	21 v 43	1600	Bayaz	JSK	SE	4	yellow	0–5	NW	small	scattered	—
27	21 v 43	1800	Anar	JSK	SE	4	yellow	0–5	NW	medium	loose	succession of flights
28	22 v 43	09–1300	Anar-Bayaz	JSK	SE	1–2	yellow	10–100	NW	large	loose	long succession of flights
29	24 v 43	1400	Riyadh	DVF	SE	1	pink	0–200	SW	medium	loose	long succession of flights
30	3 vi 43	1500	Anaristan	JSK	W	1	yellow	100–?	C	small	scattered	—
31	13 vi 43	09–1300	Yusefabad	JSK	S	2–8	pink	0–10	N	medium	dense	—
32	13 vi 43	1600	Yusefabad	JSK	S	3	pink	0–10	N	small	scattered	—
33	14 vi 43	09–1500	Yusefabad	JSK	S	2	pink	0–10	NW	large	dense	—
34	15 vi 43	1600	Burj-i-Maas	JSK	S	3	pink	0–10	N	small	loose	—
35	16 vi. 43	09–1100	Burj-i-Akram	JSK	SE	3	pink	0–5	NW	medium	dense	—
36	17 vi. 43	1400	Badaran	JSK	S	3	pink	0–10	N	small	scattered	—
37	9 vii 43	1500	Shusp	JSK	SW	2	pink	0–10	NE	medium	scattered	—
38	13 vii 43	1100	Birjand	JSK	SW	3	pink	0–10	NE	small	loose	—
39	31 iii. 43	1100	Nakuru	JSK	W	2	pink yellow	5–30	E	medium	dense	—
40	31 iii 43	1200	Nakuru	JSK	W	1	pink-yellow	0–60	E	medium	dense	several columns
41	31 iii 43	1500	Nakuru	JSK	W	5	pink-yellow	0–3	E	small	dense	several columns
42	11 iv 44	1600	Nakuru	JSK	NW	3	pink yellow	0–15	SE	medium	dense	—
43	11 iv 44	1700	Nakuru	JSK	NW	6	pink-yellow	5–15	NW	medium	dense	same as 42
44	13 iv 44	1100	Njoro	JSK	S	1	pink-yellow	0–30	N	medium	dense	—
45	21 iv 44	1600	Naivasha	JSK	NW	3	yellow	5–15	SE	small	loose	—
46	21 iv 44	1700	Naivasha	JSK	N	2	yellow	0–10	S	medium	loose	—
47	23 iv 44	1000	Morendat	JSK	NW	1	yellow	0–30	SE	medium	dense	—
48	23 iv 44	1600	Elmenteita	JSK	SE	3	yellow	0–15	NW	medium	dense	—
49	27 iv 44	0900	Elmenteita	JSK	S	1	yellow	30–200	SW	medium	dense	—
50	30 iv 44	1000	Eldalat	JSK	W	1	yellow	0–60	E	large	dense	—
51	3 v 44	0900	Eldalat	JSK	NE	1	yellow	0–200	N	large	dense	—
52	23 v 44	1400	Naivasha	JSK	N	4	pink	0–7	S	large	dense	—
53	24. v 44	1400	Naivasha	JSK	N	3	pink	0–20	S	large	dense	several swarmlets

Key to observers' initials LI, local informants, DVF, D Vesey-Fitzgerald, AGH, A G Hussain, OBL, O B Lean, ANS, A. N Scherbinovsky, TA, Taqi Ahsan.

rains generations in the Kenya highlands in March–May 1944—were fully *gregaria* in phase judging by their appearance and behaviour and by the appearance and behaviour of the hoppers from which they came

TABLE 3 FREQUENCY DISTRIBUTIONS OF E/F RATIOS OF SPECIMENS COLLECTED IN SOUTH IRAN

place	date	sex	no of specimens with E/F ratio 1 76–1 90	1 91–1 95	1 96–2 00	2 01–2·05	2 06–2 10	2 11–2 15	2 16–2 20	2 21–2 25	2 26–2 30	2 31–2 35	2 41–2 45	2 61–2 65	total
Bandar Abbas	April 1943	M	—	—	1	1	2	4	2	—	—	—	—	—	10
		F	—	1	—	1	1	3	3	1	—	1	—	—	11
Anar	May 1943	M	1	—	—	—	2	9	5	6	1	2	1	—	27
		F	—	—	—	—	1	2	3	3	3	3	—	1	16

The start of migration

As far as could be judged, the fully migrant swarms encountered in both Persia and Kenya came to rest at night and launched afresh on migration each morning This appears to be the normal although not the invariable pattern of their behaviour, and examination of that launching process should throw a direct light on the nature and causes of migratory behaviour Gunn *et al* (1948), who managed to be present at the morning departure of Desert Locust swarms on seventeen occasions, have described the launching process and, for purposes of aircraft attack, divided it into the following stages quiescence, basking in trees, basking on ground, flying about, streaming away

The present account, having a more general purpose, expands their scheme somewhat, although based on but a few observations and supported by very scanty records of accompanying conditions There were four morning observations on fully migrant swarms, and a general account of the launching process will be given before considering the observations individually

✓ The locusts spend the night roosting off the ground on trees or shrubs if there are any such perches available If it is warm there may be some movements in the growing light before sunrise, but noticeable activity begins after sunrise when the locusts move their limbs and then crawl slowly about If it is dull and cool, movements may continue sluggish for hours If it is bright, the locusts soon take up positions in the sun with their bodies perpendicular to its rays (Fraenkel 1930) This *basking* behaviour continues, among locusts not for the time being flying, from then on until the departure of the swarm Baskers are at first mainly on perches off the ground, but as the morning progresses they collect on sunny, barer patches of ground, as sheets of massed, parallel-bodied insects When crawling and basking become general, locusts begin to drop from their perches, the earlier ones mainly gliding but later ones fluttering down in a ragged rain of insects to the ground As wing-beating becomes more energetic (fuller in amplitude) those taking off from trees, etc , do not at once drop to the ground, but fly along horizontally a few metres, and some of the locusts on the ground rise from it in similar short flights Although these earliest fliers are scattered thinly through the swarm and apparently independent of one another, they may show a certain uniformity of direction

As the number of fliers and the duration of each flight increase, mutual stimulation of locust by locust becomes noticeable, and its effect, at this stage, is to make the flights more random in direction Chaotic *milling* begins, that is, loose, non-persistent flying with no signs of a common orientation, but involving enough locusts together to form a thin cloud, resembling butterflies over their food-plants The flights become steadily more energetic and prolonged and embrace more locusts They begin to take the form of *surging*, that is, temporary and local concerted flights by flocks of insects, directions differing from flock to flock, and from time to time in the same flock With further increase in the duration and vigour of flights the flocks grow larger, absorbing individual fliers and smaller flying groups

At this time there are still many locusts basking in trees and on the ground Taking off by single baskers, apparently spontaneously, can still be seen, but now whole groups of baskers take off together or in rapid procession especially when flocks of other fliers pass over

At some time during milling and surging, 'there tends to emerge a thickening uni-directional stream' (Gunn *et al* 1948, p 14) The stream is not a continuous column of fliers What happens is that, amid all the confusion, a common direction becomes increasingly apparent among individuals, groups and flocks, even when they have no evident connexion with one another The common direction may change from time to time and the locusts concerned do not fly far, but the common direction seen at this time is naturally more conspicuous than that sometimes observed before milling has become general, for the fliers are now more numerous and stay in the air for tens or even hundreds of metres

Finally, the pattern of movement in the swarm undergoes what is usually a rather dramatic transformation Resettling declines markedly and the basking locusts rise up in flocks to join their fellows sweeping overhead, leading to a sharp increase in the number of locusts in the air The fliers merge into a single great flock in the air, and at the same time they all assume the same direction and keep to it with a persistency not seen until then Gunn *et al* (1948) describe this as 'the beginning of a mass stream-away' They found it was striking enough to be fixed in time within a few minutes, but that the complete evacuation of the roosting site could take an hour or two In all the four present cases evacuation was virtually complete in 15 to 20 min Since fairly sustained, if thin, streaming can sometimes be discerned some time before the massed stream-away of the departing swarm, it is proposed to call the former *streaming* and the latter *mass stream-away* or *mass departure*

To sum up, the process may be tabulated as follows

(1) Beginning of activity—crawling

(2) Quiescent basking in the sun, perpendicular to its rays

(3) Vol-planing and hopping flights—individual and very short, but often in a common direction (thin *streaming*)

(4) *Milling* flights—short and disorderly, by many individual locusts

(5) *Surging* flights—longer and by whole groups together, but with directions varying.

(6) *Streaming*—increasingly prolonged flights in one common direction

(7) *Mass departure*—sustained, uni-directional flight embracing the entire swarm, basking locusts rising to join it

It is emphasized that while the stages are given in order of their appearance, there is much overlapping Stage 2, basking, continues through stages 3, 4, 5, 6 and into 7. The only noticeable break in the whole process is when stage 6, streaming, passes into stage 7, mass departure Then all the earlier stages, if still evident, come to a more or less speedy end.

The duration of the stages varied considerably between different days as will be seen in figure 1

13 April was a misty morning with thin cloud over the sun and the temperature rose slowly. Milling and surging involved only a minority of the locusts, the majority passing straight from basking into streaming and mass departure.

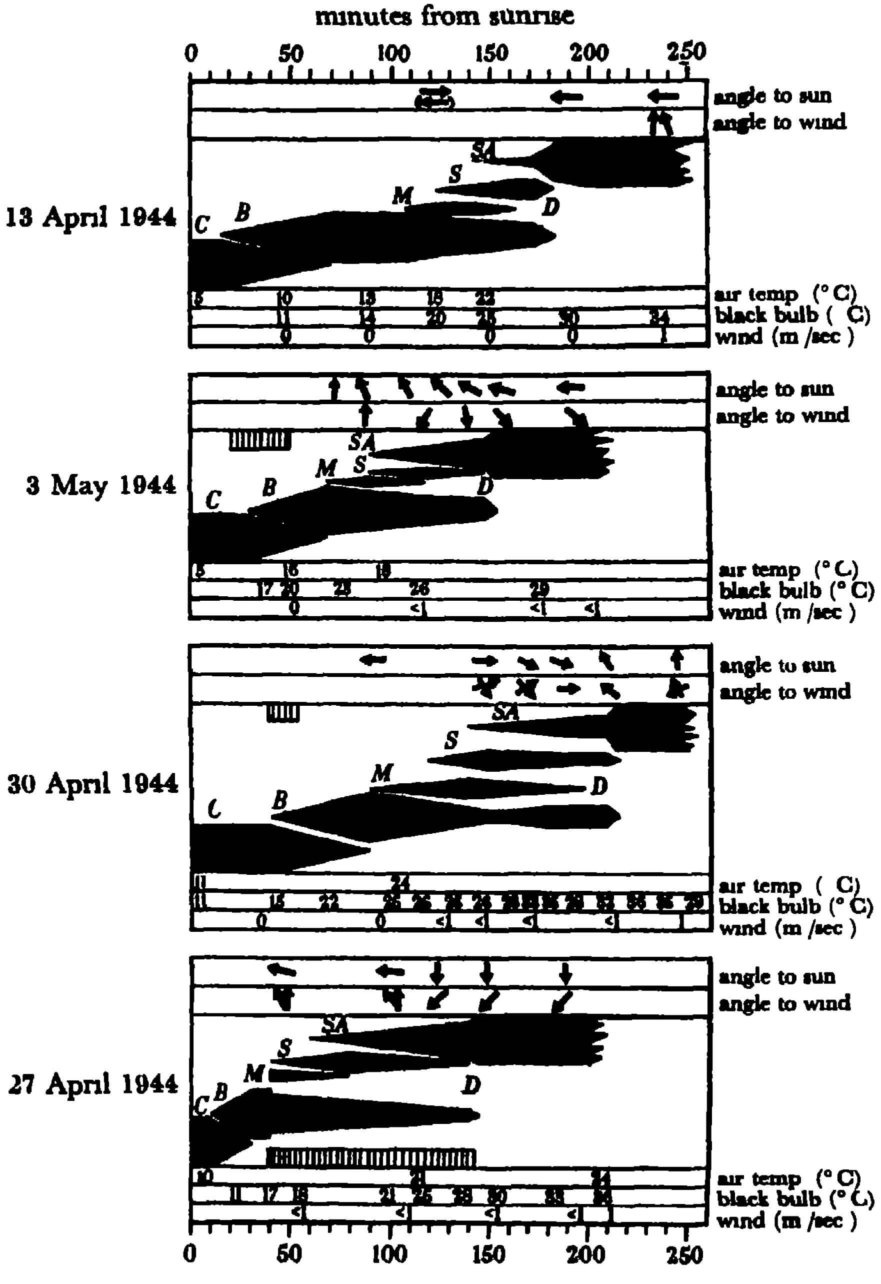

Figure 1 The morning behaviour of migrant swarms. The vertical width of each black strip is roughly proportional to the fraction of all the locusts visible that were engaged in the type of activity indicated *C*, crawling or motionless, not basking, *B*, basking, *M*, milling, *S*, surging, *SA*, streaming-away The time of mass departure is indicated by *D*. Orientations are shown along the top of each record, with the sun assumed to be at, and the wind blowing from, the top of the page. The vertically striped blocks mark the periods when aircraft were flying low over the swarm.

3 May was a clear morning and the temperature rose rapidly Milling and surging began 40 min earlier than on 13 April These stages were short-lived and involved an even smaller proportion of the locusts than on 13 April, for streaming began as soon as surging, at 90 min from sunrise Mass departure, at 150 min , was less dramatic than on 13 April because the majority of the locusts were streaming before the final spurt of taking off and the onset of sustained flight marking the mass departure

30 April was clear at first but the locusts were extremely wet, and basking had only just become general at 100 min when the sun began to be obscured intermittently Milling and surging lasted twice as long as on 13 April and 3 May with repeated mass resettling Mass departure was delayed until over 200 min from sunrise and after more than an hour's thin streaming

27 April was a clear morning, but the course of events was violently altered by disturbance from low-flying aircraft These were Avro Ansons which flew over the swarm, dusting it with dinitro-*ortho*-cresol, one after another every few minutes at heights of 3 to 10 m Dusting aircraft had also flown over the swarms observed on 3 May and 30 April, but before basking had become general (see figure 1) and without noticeable effect on the locusts On 27 April however, the low-flying started after basking had become general and continued for 100 min The insecticide dosage proved to be too low to produce any appreciable kill, but each aircraft generated the most violent flight activity among the locusts, which rose in masses in *front* of the aircraft's nose, alike when the latter was delivering dust and when it was not Milling began with the first aircraft at 40 min from sunrise and surging immediately afterwards, followed at 60 min by streaming Streaming embraced more and more locusts during the next 80 min , so that the mass departure at 140 min was not very striking, for most of the locusts were already air-borne

On all four occasions it was observed that the common direction of streaming locusts was assumed independently by separate groups and even by isolated individuals Sometimes individual locusts were observed to take up the stream-away direction while completely screened by vegetation from any sight of their fellows Streaming locusts were apparently reacting in common to some external directing agency, and records were therefore kept of their orientation with reference both to the sun and the wind (figure 1), bearing in mind the conclusions drawn from observations on hoppers (Kennedy 1945) that departure directions might be connected with basking orientation

On 13 April the departure direction was northwards, the direction in which about half the locusts were facing as they basked perpendicular to the sun's rays, but the departure direction was at the same time against the northerly wind Locusts basking with their right sides to the morning sun took off and continued to fly with that orientation into the wind Those basking with their left sides to the sun took off in that orientation, but once in the air and so exposed to the wind, they wheeled round into the up-wind orientation, with their right sides to the sun, as they settled down to steady flying The wind alone might have been regarded as setting the departure direction had it not been noticed that from the very first the orientation of streaming locusts was more fixedly perpendicular to the sun than it was parallel to the wind This swarm was kept in sight for about an hour from the time of its departure from the roosting site, for it progressed slowly owing to periods of resettling when the wind rose During that time the wind direction was not of course rigidly fixed but frequently shifted by as much as 45° Yet the locusts did not follow the shifts, their orientations remaining within a much narrower range of compass directions

On 3 May, 30 April and 27 April flight directions bore no consistent relation to the wind as will be seen from figure 1 On 3 May the departure direction, like the basking orientation, was perpendicular to the sun's rays, as on 13 April, although earlier streaming locusts had not in this case been flying perpendicularly to the sun's rays They started flying directly toward it, and the direction of streaming shifted steadily around until it was perpendicular to the rays The up-sun direction appeared originally among the earliest vol-planing and hopping fliers before basking had become general and thus could not have arisen out of a basking orientation On 30 April and 27 April, early, thinly streaming locusts flew in the contemporary basking orientation, perpendicular to the sun's rays, but final departure directions were parallel with the sun's rays up-sun on 30 April after prolonged milling and surging activity, and down-sun on 27 April after equally prolonged and even more intense surging activity prematurely induced by the low-flying aircraft

One additional point should be mentioned individual locusts were observed to flutter their wings without taking off on 30 April and 3 May Gunn *et al* (1948) observed wing fluttering one morning as a mass phenomenon among densely packed Desert Locusts on one tree, among many trees similarly packed with locusts where no wing-fluttering occurred They suggested that it was set off by jostling among the insects The present occasions were different in that the locusts were not so densely crowded and the fluttering individuals were scattered here and there throughout the swarm, so that jostling was less likely to be what set off the fluttering On both occasions, however, the locusts were very wet from rain (as they were also in the case described by Gunn *et al.*) On 13 April and 27 April, when there was no fluttering, the locusts were moist with dew but not encumbered by large rain drops

Influences affecting swarm behaviour

The condition of the locusts

First among the influences affecting migratory behaviour was evidently the condition of the locusts themselves Most of the locusts encountered during this investigation were at least several weeks old and fully hardened, but, whether pink or yellow in colour, they were not engaged in mating or egg-laying Such swarms are listed as 'full migrants' in table 1, for whenever they were observed, during most of the hours of daylight, they were in energetic flight, implying that they flew persistently through those hours A minority of the swarms encountered were composed either of recently moulted adults, or of sexually mature adults a proportion of which were observed mating and ovipositing These two conditions of the locusts themselves seemed to hinder their migration Such swarms are therefore listed as 'semi-migrants' in table 1

Fledglings Recently moulted adults, or *fledglings* as they have come to be called, were observed for eight successive days in June 1943 in the region south of Bam, south-east Iran Initially, on 9 June there were still many hoppers and newly moulted adults scattered over a large area The soft adults did not fly at all, except when disturbed, and then very briefly and feebly There were also large concentrations of somewhat older fledglings in and around the oases These were harder-bodied and flew readily, but were still perceptibly softer to the fingers than yet older, fully migrant locusts. The morning behaviour of these more advanced fledglings was watched on three days 10, 11 and 12 June 1943 (figure 2) It was very warm, as the few temperatures entered in figure 2 show Crawling activity did not stop altogether even during the night, and basking became general almost immediately after sunrise But there was no sustained flying, and no mass departure A consistent direction did appear on 10 June, which is shown as streaming in figure 2, but in fact these locusts settled with every small increase of wind. Had they remained in the air they would certainly have been turned down-wind, and such alternating orientation has been described as *surging* On 11 June, a warmer day, the locusts flew rather more uninterruptedly, rising higher in the air On 12 June they were immobilized for most of the morning by a strong wind They surged up-wind and down-wind during a brief lull at 130 min after sunrise and again when the wind dropped after 320 min

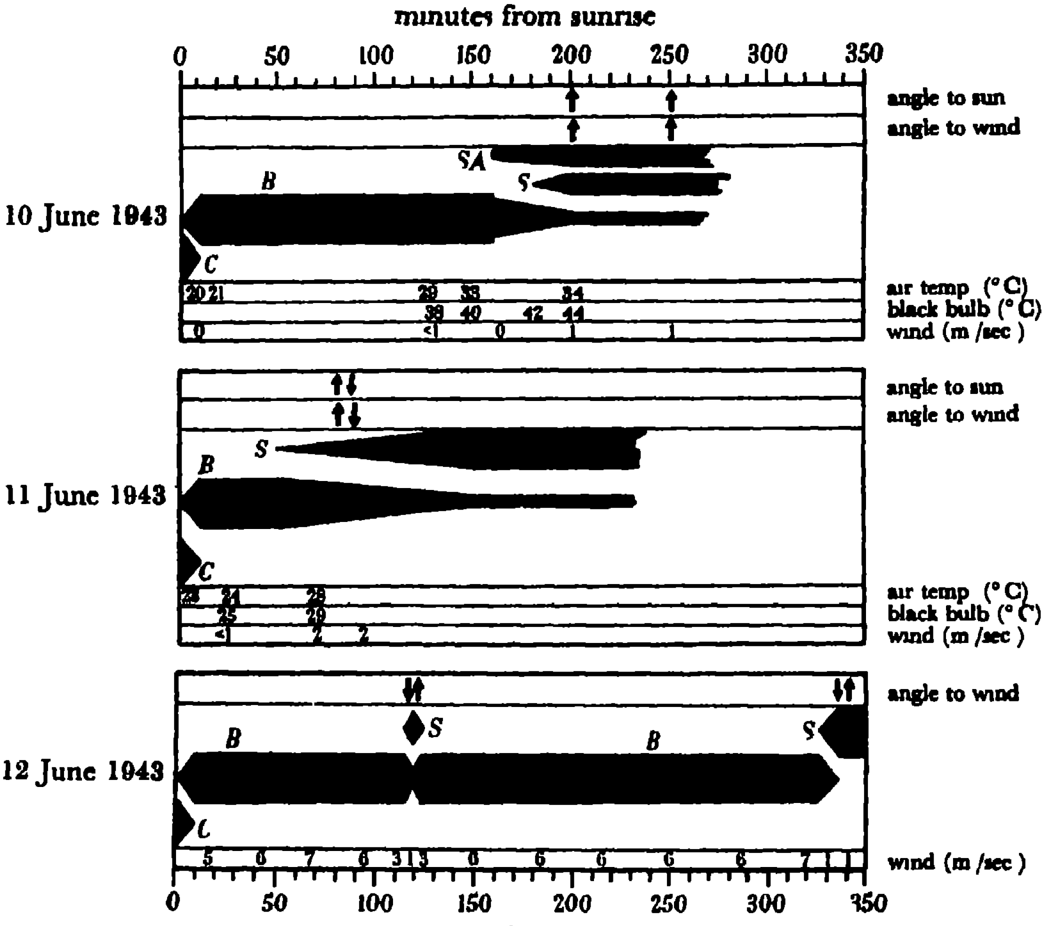

FIGURE 2 The morning behaviour of fledgling swarms Constructed as figure 1 Temperature on 12 June followed a similar course to that on 10 June

The persistence and vigour of flights increased day by day From the 9th to the 12th the locusts 'milled' and 'surged' a good deal, making little resultant progress On the 13th they had passed into a half-surging, half-migrating stage and shifted *en bloc* to a new roosting site By the 16th they had moved several kilometres, and it was clear that their behaviour would soon be indistinguishable from that of fully hardened, migrant swarms It was usually rather windy, and the fledglings flew low and against the wind They were easily driven back, turned about and forced to settle by very moderate gusts, against which older adults could have made headway In calm, warm periods they sometimes rose higher into the air, and then were swept back for considerable distances by opposing but quite gentle gusts

To sum up, the fledglings were seen to develop fully migrant behaviour gradually as they hardened Their behaviour exhibited a developmental sequence paralleling, on an extended time-scale, the morning launching process of a fully migrant swarm Inasmuch as the wind easily carried them with it or grounded them, their tendency to fly spontaneously *en masse* seemed to develop in advance of their ability to fly strongly

An isolated observation of fledglings taking to flight at dusk may be mentioned here. Fledglings were encountered again near Birjand, north-east Iran, on 10 July 1943 They flew very little in the daytime, many being quite soft, and flying had ceased altogether well before sunset At dusk the sky was clear, the air temperature was 24° C, and a light wind was blowing from the north-east A few minutes after the sun had set a large number of individuals were seen to take off one by one and fly low until out of sight Some flew against the wind, and a few in the opposite direction with the wind Most flew facing straight towards the bright western sky The number of take-offs reached a maximum about 30 min after sunset and then declined gradually until it had ceased entirely a few minutes before it would have been too dark to see the locusts against the sky The great majority of the swarm remained where they were for the night It was not observed whether such dusk take-offs occurred also at Bam in June

Mating and ovipositing swarms The behaviour of mating and ovipositing swarms was observed for several hours from sunrise on four occasions in Iran in 1943 at Anar on 22 May, at Kabutar Kahn (between Anar and Kerman) on 26 May, and near Rayin (south of Kerman) on 31 May and 1 June Another such swarm was observed for some hours on the western shore of Lake Naivasha, Kenya, on 22 April 1944 Detailed notes were kept on the last three occasions which are illustrated in figure 3

There was no mass departure on any of these days, but a long-drawn-out trickling away by individuals or loose groups which often flew up-wind for short distances but were repeatedly carried and thereupon turned down-wind, even by weak winds These flights are entered as 'surging' in figure 3, but were much less dense and at first less energetic than the usual surging flights of full migrants already described Many of the locusts were still on the ground when observation ceased, and by no means all of these were engaged either in mating or in egg-laying Many were simply sitting quietly in the sun

On 31 May there was little copulation and no oviposition to be seen The swarm watched on the next morning was very possibly the same one Numerous copulating pairs and ovipositing females with males on their backs were found in the latter swarm during the earlier part of the night 31 May–1 June Later the cold immobilized them, and many females were found torpid with their abdomina inserted in the ground Mating and laying became general again during the following morning while scattered fliers were leaving This swarm, like the one observed at Anar on 22 May, contained many more males than females when inspected during the first hour or so after sunrise Many of the females and a few of the males were found dying Some hours later on 1 June the sexes were found to be present in

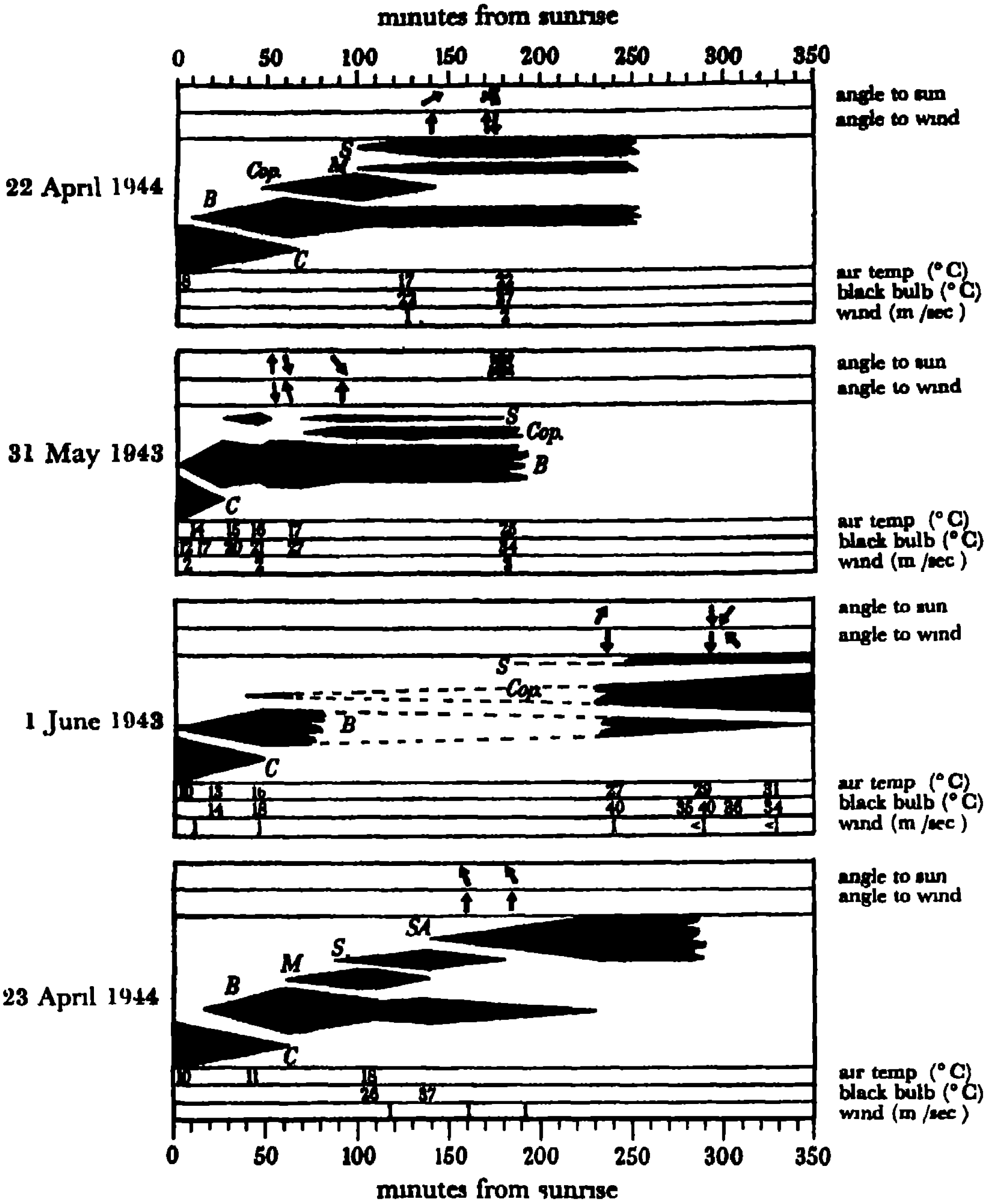

FIGURE 3 The morning behaviour of copulating and ovipositing swarms Constructed as figure 1 *Cop* copulating

nearly equal numbers among the remaining locusts, showing that it had been mainly males that had flown away On this day the departing fliers flew sufficiently vigorously and sufficiently in a common direction, down-wind, to be described as streaming, but they did so very loosely and over a much longer time than that occupied by the mass stream-away of fully migrant swarms already described

The swarm observed in Kenya on 22 April 1944 also streamed slowly away on the wind in this fashion On both these days it was observed that while some fliers were streaming near the ground, others were flying to and fro higher up over the roosting site The latter increased in number until they formed a large but very thin milling cloud of locusts As time went on this cloud extended higher and higher into the sky, many individuals being detectable only when the sun caught their wings as they passed between it and the observer The high fliers eventually lost connexion with those near the ground, leaving an intermediate stratum clear of locusts and two totally different types of flying going on at the same time, uni-directional below and multi-directional above

The swarm observed in Kenya on 23 April 1944 may have been the same one as that watched departing the previous day Local observers believed it had been mating and laying for several days previously at various points in the vicinity, but no mating or laying was seen during the 4 hr the swarm was watched on 23 April This observation is included here because the locusts' behaviour was peculiar, being intermediate between that of a fully migrant swarm and that of a mating swarm Unlike the locusts from mating swarms, these showed well-defined milling and surging behaviour and departed in a fairly thick stream against the wind without forming a high-circling detachment, and they had evacuated the roosting site altogether after 3 hr For that reason their departure is shown as streaming in figure 3, but there was no mass departure The departing stream was looser and more ragged than that of fully migrant swarms, basking was long-drawn-out, and the swarm took 40 min longer to evacuate its roosting site than the slowest of the fully migrant swarms (figure 1), although the weather was warmer

All these swarms showed a weakened tendency to take off either individually or *en masse* Unlike fledglings, they were, however, capable of vigorous flight when pursued The restriction of migration was associated with sexual activity, but was not simply due to the replacement of flying activity by copulation and egg-laying, for there were always many locusts not doing either of these things and still not actively migrating

Wind

Speed of flight When, as frequently happened, full migrants were seen flying very low into the wind, their ground speed (speed relative to the ground) seemed to show a measure of independence of variations in the wind speed This was merely an impression, for only the wind speed and not the insects' speed was measured, but the impression was very strong When the wind increased or decreased, low up-wind fliers did not appear to slow down or accelerate proportionately but rather to maintain a relatively unchanged ground speed in winds up to 4 m /sec (9 m p h) or more If they did maintain roughly the same ground speed against such a range of wind speeds, the locusts must have adjusted their air speed (speed of movement relative to the air) to the wind speed Judging by the speed of wind gusts which, suddenly meeting the locusts, carried them momentarily backwards, the cruising air speeds of locusts flying against light winds varied between 2 5 and 4 m /sec

The impression that low fliers were regulating their ground speed by adjusting their air speed according to the wind speed, was strengthened by a further impression that higher fliers were not so adjusting their air speed, so that their ground speed was more closely dependent on the wind speed The fact that higher fliers appeared to be more easily slowed down and even carried backwards than low fliers in the same gust, might, of course, be attributed merely to the fact that the wind is stronger away from the frictional drag of the ground But higher fliers appeared also to surge forward more freely when the wind dropped, which could not be explained in the same way, and suggested that they were actually exercising less control over their ground speed, that is, maintaining a more unchanging air speed

Amount of flying and height of flight Low-flying migrants showed a clear tendency to regulate the amount of flying they did and the height at which they flew, according to the wind speed Increase of wind speed to the point where down-wind orientation supervened (p 184) did not noticeably affect the locusts if the increase was only momentary, and there was a quick return to up-wind orientation More prolonged exposure to a wind of this or greater strength, however, led to a decrease in the height of flight or even to complete settling If the locusts made headway against the wind at the lower flight level, owing, presumably, to the wind being slower near the ground, they flew on, keeping low If not, they settled Some particular incidents may be quoted to illustrate these effects

On 20, 21 and 22 May 1943, a succession of scattered individuals and swarmlets of mature locusts (table 2, nos 20–28) were observed moving in a north-west direction up the Kerman-Anar road against a wind of 1 to 3 m /sec At about 1300 hr on 22 May the wind increased to 3 to 6 m /sec and remained at that level without any other changes in the weather, whereupon flying ceased and only settled locusts were seen for the rest of the day's journey

On the afternoon of 24 May 1944 a large, rather loose, immature swarm was watched on the shores of Lake Naivasha It had crossed the lake in intermittent sun, flying at 5 to 30 m above the water and against a wind of 2 to 3 m /sec Part of the swarm had already reached the shore and passed on over the land, when the wind increased to 4 to 5 m /sec Thereupon most of the locusts that were over the land, especially the lower fliers, flew on against the wind and dropped lower still For many minutes afterwards the numbers in the air over the land, and the level at which they flew, rose and fell repeatedly in inverse relation with the rise and fall of the wind speed Then, heavy rain began to fall on them, with a drop in temperature, and some further increase in wind The locusts dropped even lower, disappearing among the trees, and did not rise into view again Two hours later they were found about 1 km up-wind of where they had disappeared, showing that they had not been entirely settled during the rain, but had continued low, up-wind flight whenever the wind permitted A similar series of descents and ascents associated with alternate periods of stronger and weaker wind, respectively, was observed over the land on the opposite (northern) shore of Lake Naivasha on the previous day

On the morning of 31 March 1944 several small, maturing swarms (table 2, nos 39–40) were seen near Nakuru, Kenya, flying in intermittently sunny conditions The level of flight ranged from near the ground up to 60 m A few hours later it began to rain rather heavily, the temperature dropped and the wind increased to a stiff breeze Two swarms (table 2, no 41) were seen in the rain, very probably the same as had been seen earlier In both cases the majority of locusts were settled at any one moment, but there was constant taking off by a minority who flew strongly against the wind, mostly keeping less than 1 m above the ground and settling again when they could not make headway Now and then individuals rose higher in the air, but came down again as soon as the wind began to sweep them back

The start of flying by massed fledglings on the morning of 12 June 1943 (figure 2) was delayed for a long time in comparison with what happened on 10 and 11 June 1943, solely, it seemed, because of an unusually strong wind, for otherwise the weather was similar on the three days As soon as the wind dropped, 'volleys' of locusts took off simultaneously at different points in the settled swarm, and the whole swarm rose quickly

There were many observations of migrating swarms during which only one or two pronounced changes of wind speed occurred, and no quantitative records were kept It was seldom possible to keep a migrating swarm in sight for long enough to observe the effects of repeated, large wind-speed changes on flight activity, as was done on 13 April 1944 (p 172) and 24 May 1944 (p 178) But it can be stated with some assurance that whenever a low-flying swarm was observed in windy weather, its flight activity (the proportion of insects flying) and its height of flight decreased when the wind rose and increased when it fell Settling due to an increase of wind speed was evidently merely the extreme case of flying lower from the same cause

The immediate reduction in the height of flight when the wind increased was seen only among locusts already flying within a few metres of the ground Members of the same swarms that were flying rather higher than that also responded, but more slowly and irregularly The effect of wind changes on swarms flying yet higher, and completely out of touch with the ground, was not observed, but it is noteworthy that there was usually little wind at ground level when fliers were seen so high

Attempts were made to obtain more quantitative data from fledglings, whose persistent but weak flight activity meant that opportunities often arose of observing them in winds against which they could not make headway Unlike full migrants, which were usually able to make some headway against the moderate winds prevailing during most of the observations, low-flying semi-migrants were often completely immobilized by such winds The absence (see table 8, p 191) of any cases of flight by semi-migrants in winds of 4 or more m /sec illustrates the immobilizing effect of even moderate wind on these fliers

Records were made of the flight activity of advanced fledglings on 13–14 June 1943, at Yusefabad, south of Bam, south-east Iran They were migrating actively, but kept low and were very sensitive to wind-strength changes Six series of minute-to-minute readings were taken of wind strength and flight activity Two of the series are shown in figures 4 and 5 A regular relation between wind speed and flight activity could hardly be expected in these records, because the wind-speed variations were irregular and too rapid to be recorded in full The unfaithful recording of short, high-wind-speed periods was especially misleading, for these had a noticeable effect upon the locusts Also, the responsiveness of the locusts varied with their height, which could not be recorded conveniently at the same time

However, the main blocks of activity (*AA*) are fairly clearly associated with weaker wind periods 2 to 4 m /sec in figure 4 and 0 to 1 5 m /sec in figure 5, while the main blocks of lesser activity (*BB*) are associated with stronger periods 4 m /sec in figure 4 and 1 5 m /sec in figure 5 And on a shorter time-scale, there are many cases where a decrease of wind speed is followed by an increase of locusts flying (corresponding *odd* numbers on the figures), and where an increase in wind speed is followed by a decrease of locusts flying (corresponding *even* numbers) Thus the changes in activity level seemed to depend not so much on the absolute wind speed as on changes in the wind speed, which often took effect in less than a minute. The apparent failure, according to the records, of gusts always to reduce activity instantly was partly due to the fact that although all the locusts responded to a gust, not all

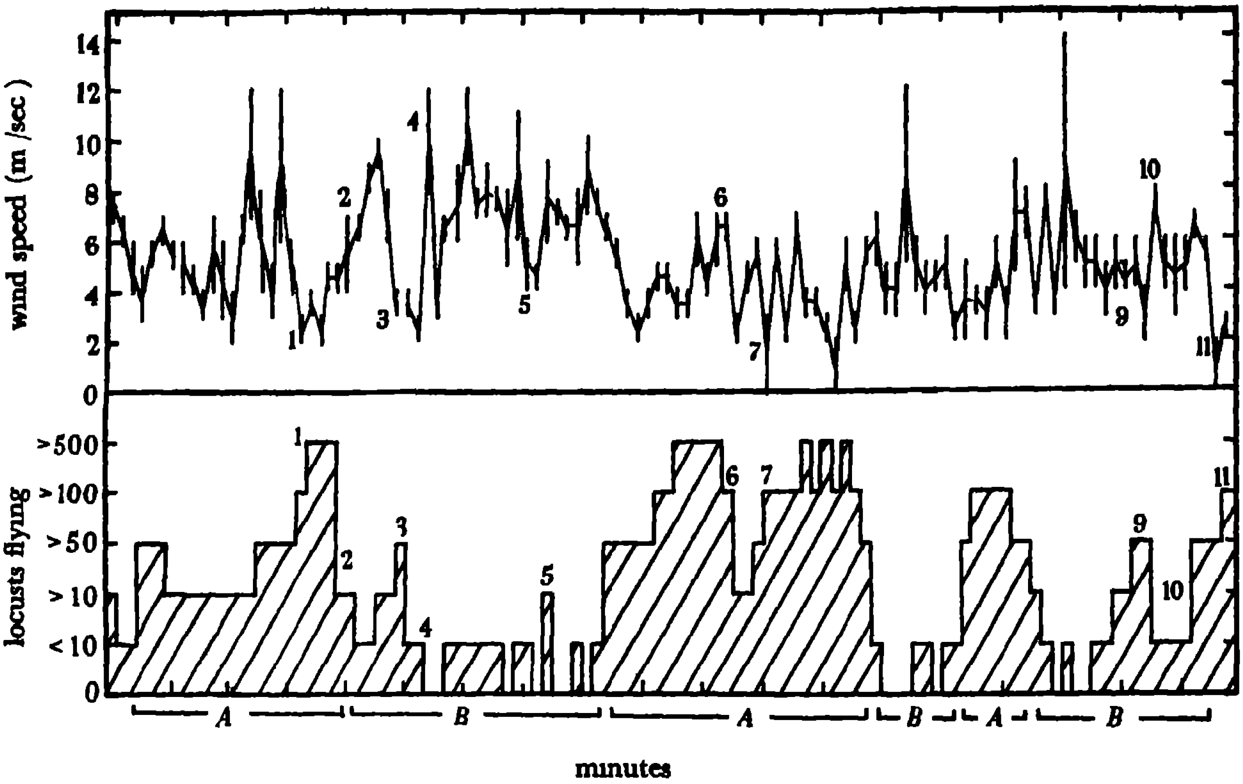

FIGURE 4 Wind speed and flight activity among fledglings Instantaneous readings of wind speed, taken every 10 seconds with a swinging ball anemometer, and simultaneous rough estimates of the number of locusts flying in front of the observer 09 10 to 09 29 hr, 13 June 1943 For lettering and numbering on figure, see text

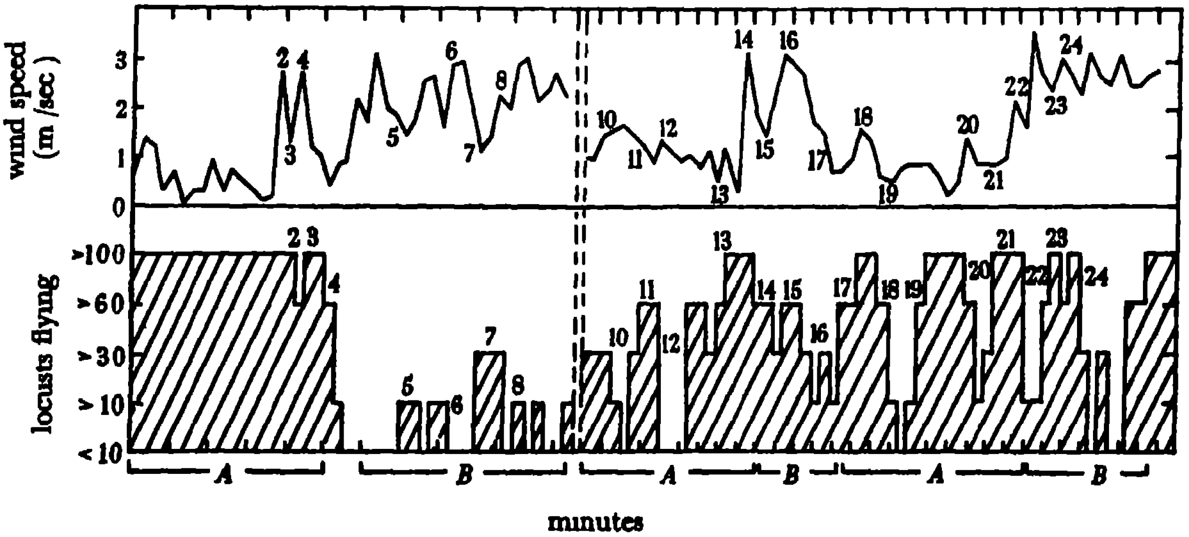

FIGURE 5 Wind speed and flight activity among fledglings Mean wind speeds during the previous 15 sec (up to the break in the record) or 30 sec (after the break), taken from the readings of an integrating (windmill type) anemometer, and rough estimates made during the same periods of the number of locusts flying in front of the observer 14 19 to 14 30 hr, 14 June 1943 For lettering and numbering on figure see text

settled at once Some, especially those rather higher in the air, were carried a little distance with the wind, turning as they went Thus it sometimes happened that, after the onset of a gust, mass settling by the locusts in front of the observer was masked in his counts by the sudden appearance of a fresh group of locusts brought on the gust and destined to settle, if the gust persisted, beyond the narrow limits of the arc to which he confined his gaze for counting purposes

Again, during brief, shallow lulls after the average wind speed had risen the locusts taking off from the ground in front of the observer were sometimes added to in the air by others surging temporarily forward again from beyond the observation area, thus exaggerating the effect of the momentary lull as a flight-evoker and masking the effect of the increased average wind speed as a flight-reducer But, apart from these complications due to influxes of locusts from outside the observation zone, those in that zone seemed to respond even to very temporary changes of wind speed, over very different ranges of absolute wind speeds This is reflected, although imperfectly, in figures 4 and 5

Thus both the long- and short-term effects of wind on flight activity seemed to be effects of *changes* in the wind speed A drop in wind speed led to an outburst of flying not only when the level to which the wind dropped was low, but also when it was quite high This was often noted, and might mean that the wind excites the insects even while it temporarily suppresses their actual flight activity That was the impression gained during some previous observations on non-gregarious locusts (Kennedy, in preparation) and strengthened by watching fledglings a few days before the above records were taken, on a day of pronounced gusts and lulls When a gust came most fliers settled on the solid ground, but some settled on trees, etc , where they were exposed to direct buffeting by the wind as well as being shaken by the movements of their perches, such as palm leaves These exposed locusts took off again in any momentary pause in the wind, or even without one, while the rest, secure on the ground, remained there until there was a good lull Thus, both sets of locusts gave up flying when the wind increased, yet the ones that came to rest where there was more wind, took to flight again sooner An extreme case, when the excitatory effect of wind became apparently completely dominant over its inhibitory effect, was observed at Jask on the Iranian coast during several days of April 1943 (table 2, nos 6 and 10) Winds were then quite exceptionally violent and the locusts seen were almost all flying (see p 183)

There is some further, if indirect, quantitative evidence on the flight-reducing effect of wind All the occasions when migrants were observed, listed in table 2, have been retabulated in table 4 in terms of the height of flight and the ground (1 5 m) wind speed which were typical or predominant on each occasion On many occasions other combinations of height and wind speed were temporarily but commonly seen, especially when the wind was gusty These further, 'frequently occurring' combinations are added to the 'predominant' ones to make up table 5 In both tables and in figure 6, where the data in table 5 are shown graphically, the percentage of high-fliers decreases and that of low-fliers increases as the wind speed increases. The height-reducing effect of stronger winds is reflected also by the absence from table 8 (p 191) of any cases of semi-migrants flying higher than 8 m in winds exceeding even 2 m /sec

The quantitative records are, however, inadequate to support the stated conclusions on the effects of wind on the amount, height and speed of flight The conclusions rest mainly on impressions and it is desirable that more precise data should be obtained by better methods under a variety of conditions

Table 4 Heights of flight according to ground wind speed Full migrants only Data for predominant behaviour, from Table 2

wind speed (m /sec)	frequencies low (<8 m)	 higher (>8 m)	 % low
<1	7	9	44
1–<4	26	16	62
4+	15	7	68

Table 5 Height of flight according to ground wind speed Full migrants only Amplified data including frequently occurring as well as predominant behaviour

wind speed (m /sec)	frequency distribution % by height of flight (m) <2	 2–7	 8–30	 >30	 no obs
<1	25	29	26	20	72
1–<4	32	39	24	5	73
4 7	39	33	18	10	49
no obs	60	65	46	23	194

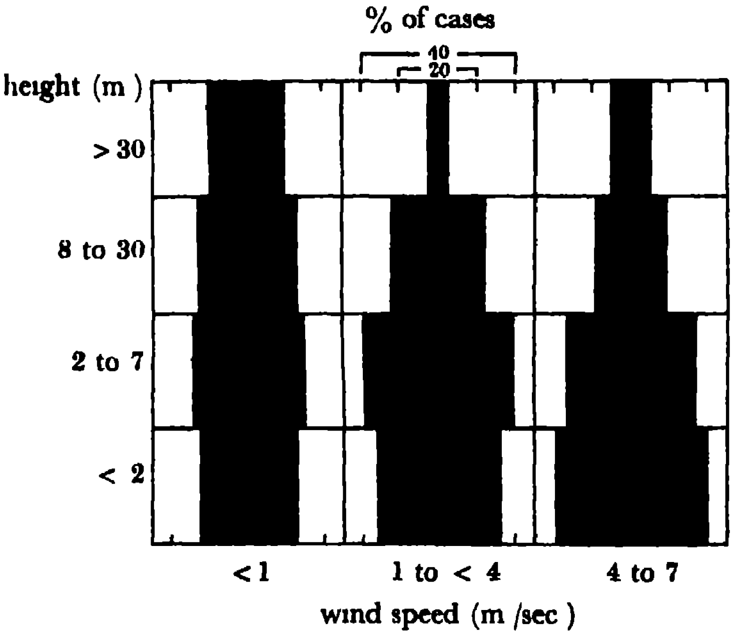

Figure 6 Frequency distributions of observed heights of flight among fully migrant swarms in different wind speeds Data from table 5 Horizontal width of each block proportional to the percentage of records for that height range, out of the total for the indicated wind speed range

Direction of flight The majority of swarms observed were migrating roughly against the wind as can be seen from table 2 and the last line of table 6 (p 190) The next most frequently observed direction was the opposite one, with the wind The wind was, however, sometimes negligibly weak, and sometimes strong enough to interfere noticeably with the locusts' flight It was obviously insufficient to record the relation between wind direction and flight direction in the hope of finding regularities without at the same time noting the wind speed Some incidents will serve to illustrate the effect of wind speed on direction

On 11 April 1944 a swarm (nos 16 and 17, table 2) was observed near Nakuru, Kenya, progressing slowly in dull weather against a 3 m /sec wind from the south-east for about 1½ hr The wind increased suddenly to about 6 m /sec, without any other weather change, and the swarm was swept back with it and reoriented down-wind, covering 12 km in at most 20 min (10 m /sec, 23 m p h) before it settled for the night

In the spring there is typically a strong northward and north-westward trend of migration in Iran (Predtechensky 1935 *a*), and swarms were repeatedly observed (table 2) flying in that direction, roughly against the wind when its speed was moderate Occasionally swarms were seen during short periods of stronger wind blowing from the same direction (table 2, nos 24, 25 and 43), and these swarms were flying with the wind

In March 1944, an extremely rapid movement of swarms took place across central and south-east Arabia, the Persian Gulf, south Iran and on into India O B Lean (unpublished records at Anti-Locust Research Centre), then in south Iran, noted that the passage of these swarms coincided with a spell of exceptionally strong winds from the west In the previous year a similar, very fast, eastward migration of young swarms took place, which cleared the coastal areas of western Iranian Mekran and led to the infestation of Pakistani Mekran In that year, 1943, Messrs N A Janjua and A G Hussain were stationed at Jask and were able to watch the locusts actually leaving (table 2, nos 6 to 10) They reported that a wind of gale force blew on 13 to 17 March from the west, that is, across the prevailing seasonal wind, and in the course of those days the area was entirely cleared of locusts The locusts were seen being tossed and swept along, orientated down-wind and with their wings sometimes actually blown forward over their heads

The *height* at which locusts were flying also seemed to influence their flight direction relative to the wind direction Different flight directions were sometimes observed in the same swarm at different heights above the ground The lower fliers in a swarm which met a strong wind near Lake Naivasha on 24 May 1944 have already been described (p 178) as coming lower and continuing their up-wind progress, but at the same time the higher fliers were carried and turned down-wind and some eventually passed out over the lake again Another swarm, about 2 km in diameter (table 2, no 48), was watched over land to the east of Lake Elmenteita on 23 April 1944 Most of it was in a hollow bounded on the north-east by a steep slope The bulk of the locusts were flying low against a wind from the north-east As soon as they reached the top of the ridge the locusts encountered a stronger wind, lost headway, wheeled and were swept rapidly back with the wind At times these recoiling locusts formed a definite stream with a common down-wind orientation, at others they formed only loose disorderly groups In either case they sooner or later came lower, turned and rejoined the main stream moving up the slope below them But the locusts moving down-wind extended far back over the main swarm so that there were two layers of locusts, a dense lower one flying up-wind and a thinner upper one drifting and sometimes oriented down-wind. More transiently and on a smaller scale the same arrangement of lower up-wind fliers and higher down-wind fliers was observed many times

Winds are stronger higher up, away from the frictional drag of the ground, and down-wind flight might be expected to appear more often at greater heights on these grounds alone But there were occasions when higher fliers were moving about at random while lower fliers were moving either up-wind or down-wind, predominantly the latter This was seen on 20 May 1943, 1 June 1943 and on 22 April 1944 (see p 177), when the different behaviour of higher locusts could not be explained by the stronger wind aloft

There were many other occasions when a swarm was watched for some time while the wind speed varied with evident effects on the locust's behaviour The actual course of such behaviour changes could not be recorded in quantitative terms, but the following general account represents the observer's firm impression from all the observations Without some such direct evidence of orientation reactions to wind, little value could be attached to the more quantitative but indirect evidence on the same subject which is quoted later

For this account, the terms *course* and *track* are borrowed from navigational language, as was done by Gunn *et al* (1948, p 44), whose definitions may be repeated here

'The *course* of a locust is the direction in which it is heading and in which its body is orientated, its speed relative to the air mass around it is its *airspeed* The direction of its movement relative to the ground is called the *track* and the corresponding speed is the *ground speed*'

The locusts were most commonly seen flying low and roughly against the wind When its speed increased and they seemed to increase their air speed as already described (p 177), they held tenaciously to their orientation, directly or more often slightly obliquely, into wind In consequence their directions remained fairly steady and parallel as between locust and locust *as long as the wind remained moderate in speed* When the wind speed reached 4 to 5 m /sec , however, the locusts' behaviour became noticeably erratic Their directions varied from moment to moment and from locust to locust as gusts came and went, although tending always to return to the old direction, with the swarm as a whole progressing into and across wind by what Gunn *et al* (1948, p 15) have aptly termed a 'rolling' action

Close attention to the behaviour of individuals under such strong-wind conditions led to the following conclusions about the detailed course of events The locusts did not always increase their air speed sufficiently, or sufficiently quickly, when hit by a gust, to prevent themselves being carried backwards But they were never seen to be carried backwards for more than a moment, for at such wind speeds, before or after backward carriage had occurred detectably, they either settled (p 178) or turned away from their up-wind orientation, toward the same side as their track had already been deviated from that course by the wind It was as if they were pursuing their own runaway tracks

Locusts which thus turned away from the up-wind orientation did not always turn right round and fly due down-wind They often stopped turning when they had attained an orientation in which there was at least no backward component in their movement over the ground, although there was a greater or lesser degree of sideways drift Consideration of the vector quantities involved shows that by turning aside in this way, the locusts reduced the chances of gusts introducing a backward component into their movement relative to the ground, even without further increase of air speed on their part, and, having so turned, the increase of air speed required to eliminate any backward component imposed by a gust was smaller than that required while oriented directly into the wind

The deviated locusts sometimes continued on a cross-wind course, until the wind slackened again, whereupon they reverted to an up-wind course The cross-wind orientation seemed to be relatively unstable and transient, however, for if the wind did not drop and allow the locusts to turn up-wind again, they commonly continued the down-wind turn and took up a due down-wind course If after this the wind still did not slacken they apparently came down and settled Fliers were always seen to turn into the wind just before alighting, even if they were not so oriented previously

Higher fliers showed the same general behaviour pattern as lower ones, but it was distinctly more 'ragged' They were thrown into greater confusion when hit by a gust than lower fliers hit by the same gust, resisted being drifted backwards less tenaciously and turned down-wind less quickly when being carried backwards After a gust had passed, higher fliers did not return to up-wind orientation as rapidly as lower fliers Since, in spite of the fact that wind speeds are greater aloft, away from the frictional drag of the ground, higher fliers were nevertheless less responsive than lower ones when hit by the same gust, it was concluded that markedly stronger winds were required to evoke responses from the higher fliers

The behaviour of fledgling and sexually active locusts, classified as 'semi-migrants' (p 173), in wind, was in principle the same as that of full migrants, with the important difference that the wind speed causing them to lose headway, turn down-wind and settle was decidedly lower than for full migrants

The same general pattern of behaviour in wind, whether of full migrants or semi-migrants, was characteristic of single, isolated fliers and not merely of dense swarms There were some differences between scattered and dense swarms, which will be dealt with under 'gregariousness'

Although no more precise method was available for recording the actual progress of the locusts' responses described impressionistically above, a method was devised for obtaining more quantitative 'snapshot' data on the course, track and height of selected individuals at given moments, with simultaneous readings of the wind direction and speed It was impossible for one man to record all these items simultaneously, and it proved inaccurate and exhausting to read course and track by looking up at the locusts and then down at a compass The method used required three persons One recorded the readings called out to him by the other two, of whom one watched the anemometer, calling out the wind speed and direction at once every time the third man called out his readings of locust directions The anemometer was of the swinging-plate type, an Italian model having a light aluminium sphere instead of a plate and giving instantaneous values for wind speed and direction at 1 5 m above the ground Throughout the present account, contrary to the conventional practice followed by Gunn *et al* (1948), the direction given for the wind is that *toward* which it was blowing, so as to conform with the way of giving locust directions

The third man took readings on what may be called the 'flight direction-finder' (figure 7) This consisted of a plate glass mirror 35 cm square laid face upwards on a suitable support In the centre of the mirror a spindle was fixed and on it was pivoted a horizontal grid of wires The centre wire was elongated so that its tip passed over a scale of degrees marked on the mirror Having first oriented the mirror with respect to the compass, the observer had only to pick out a particular locust seen passing across the mirror, quickly set the grid so that the wires lay parallel first with the course and then with the track of the locust, and call out the readings obtained It would have been an advantage to have had a small swivelling telescope attached to the apparatus for readings from high-fliers

Before considering the whole collection of separate records of flight direction in relation to wind speed and height, a few series of records taken from single swarms may be quoted These merely supplement, and cannot fully take the place of the impressions formed at the time, so that the two must be given together But these disconnected 'snapshot' records may be taken as partially illustrating what has been described above as the general impression, and as showing the possibilities of a method which requires further elaboration before it can be used to provide quantitative information on the continuous *process* the observer sees

Figure 8 shows four sets of records from full migrants between Anar and Kerman, Iran, on 20 to 22 May 1943 The course and track of each individual, the direction toward which the wind was blowing and the wind speed at the same moment, are all entered at the same point along the horizontal time axis, that is, in one vertical row Readings were taken in

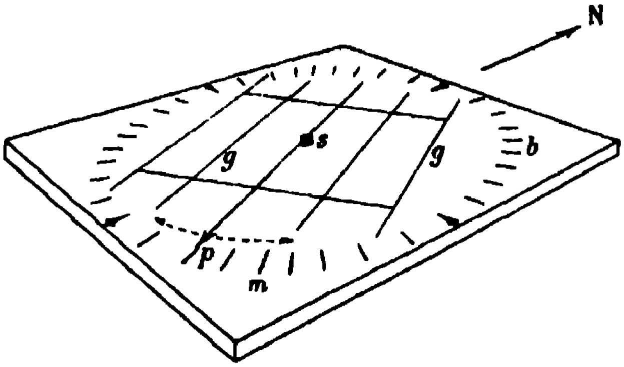

FIGURE 7 Diagram of the 'flight direction-finder' *m*, mirror, oriented with reference to the compass, *s*, spindle bearing *g*, rotatable grid of wires of which the centre one projects to form a pointer *p*, moving over the scale of bearings *b*, marked on the mirror at 10° intervals

the order shown, but not quite at the regular time intervals shown The successive readings are connected up merely to guide the eye, having been taken from different individuals It is emphasized that the records were not taken at random, individuals being selected with a bias toward those temporarily deviated from the predominant direction, and toward moments when the wind was exceptionally strong

In series *A* (44 min duration) the wind was weak, usually 0 to 2 m /sec , and usually blowing to 120° but variable in direction The locusts were flying almost exactly against the mean wind direction, and even those selected for recording nearly all kept their courses steady, sudden wind accelerations or direction changes causing only sporadic deviations of track from course

In series *B* (24 min) the wind was stronger than in *A*, usually 1 to 3 m /sec , but steadier in direction The locusts were flying slightly to the left of due up-wind most of the time, and again even selected ones kept their courses nearly steady, but their tracks were often temporarily deviated by changes of wind speed and direction

In series *C* (24 min) the wind was generally higher and steadier in speed than in *B*, about 3 m /sec , but made a marked directional diversion away from its normal, and back again, during the period when the readings were taken Most of the locusts were flying somewhat to the left of directly against the normal wind direction, but their courses were rather more variable than in series *B* These variations were smaller, however, than the changes in wind direction, and the locusts' tracks were not always and not greatly different from their courses

In series *D* (24 min) the wind was stronger even than in *C*, 3 to 7 m /sec , although steadier in direction On the average, the locusts were flying slightly to the right of due up-wind, but their courses here changed with changes in the wind and their tracks were nearly always deviated from their courses

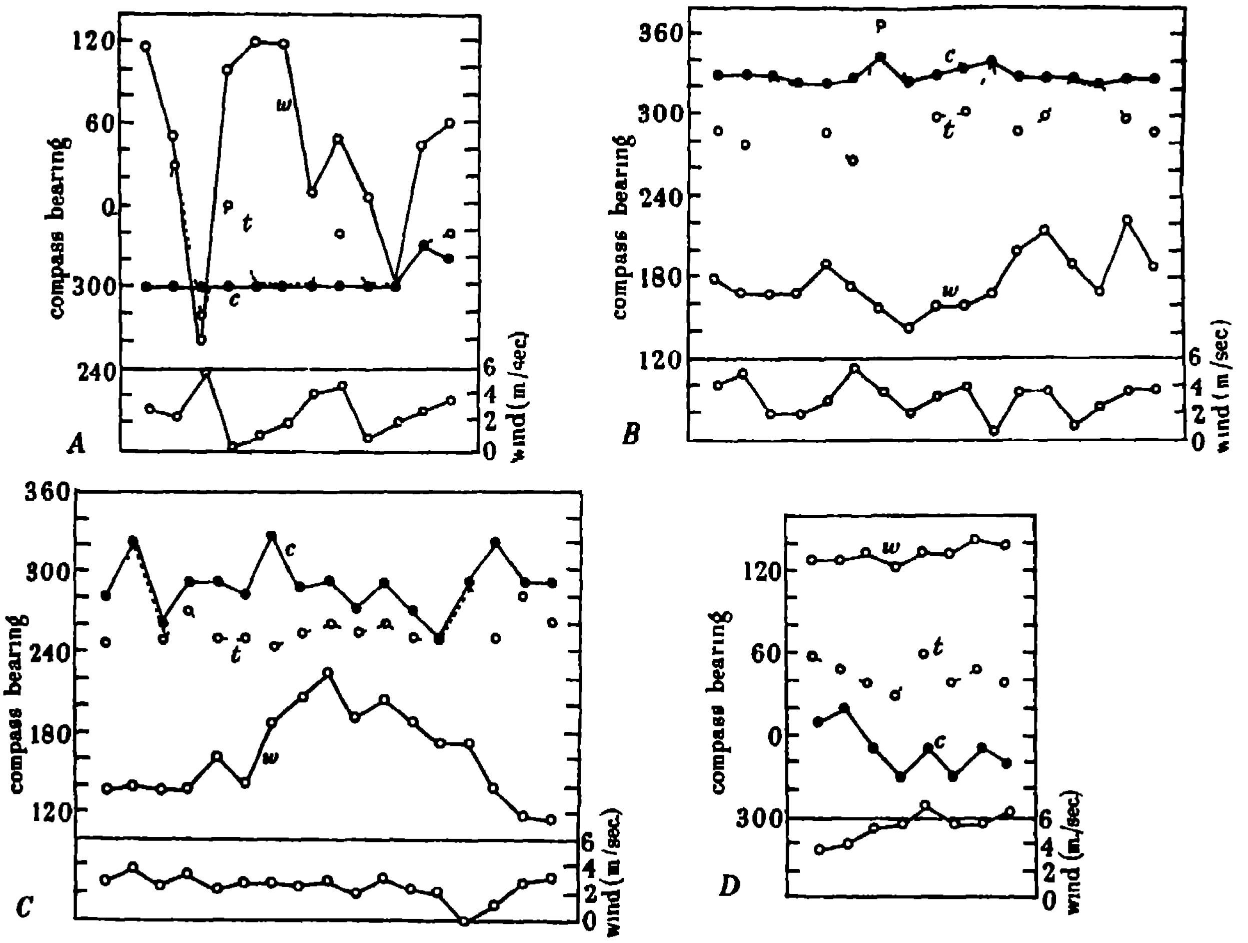

FIGURE 8 Individual direction-readings from successions of locusts flying at 1 to 4 m above the ground in swarms migrating roughly against the wind in full sun *c*, course of locust, *t*, track of locust, *w*, direction toward which wind was blowing For further explanation see text, p 186

To sum up, the locusts adhered firmly to their set courses roughly against the mean wind direction, despite deviations of track when the wind accelerated, unless the wind speed exceeded 4 m /sec , when their courses became distinctly erratic

The readings taken from full migrants do not include any examples of their turning right round and flying with the wind, although this was not infrequently seen, especially among higher fliers Such complete reversals were observed more often among fledglings, because they were thrown into confusion by the more commonly experienced, weaker winds against which full migrants made steady headway Readings taken with the flight direction-finder from fledgling swarms in the region south of Bam, south-east Iran, are shown in figures 9 and 10.

The swarm from which the readings shown in figure 9 were taken consisted of advanced fledglings making very slow, rolling progress against the wind through an open tamarisk grove on 16 June 1943 Flocks of the locusts took off and surged forward whenever the wind

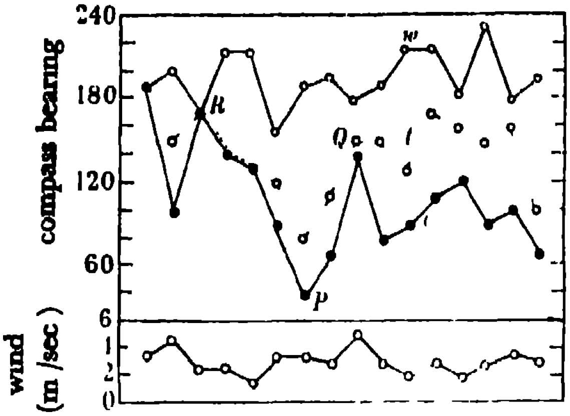

Figure 9. Individual direction readings from fledgling locusts flying within 3 m of the ground and deviated from their initially up-wind tracks by the wind Constructed as figure 8

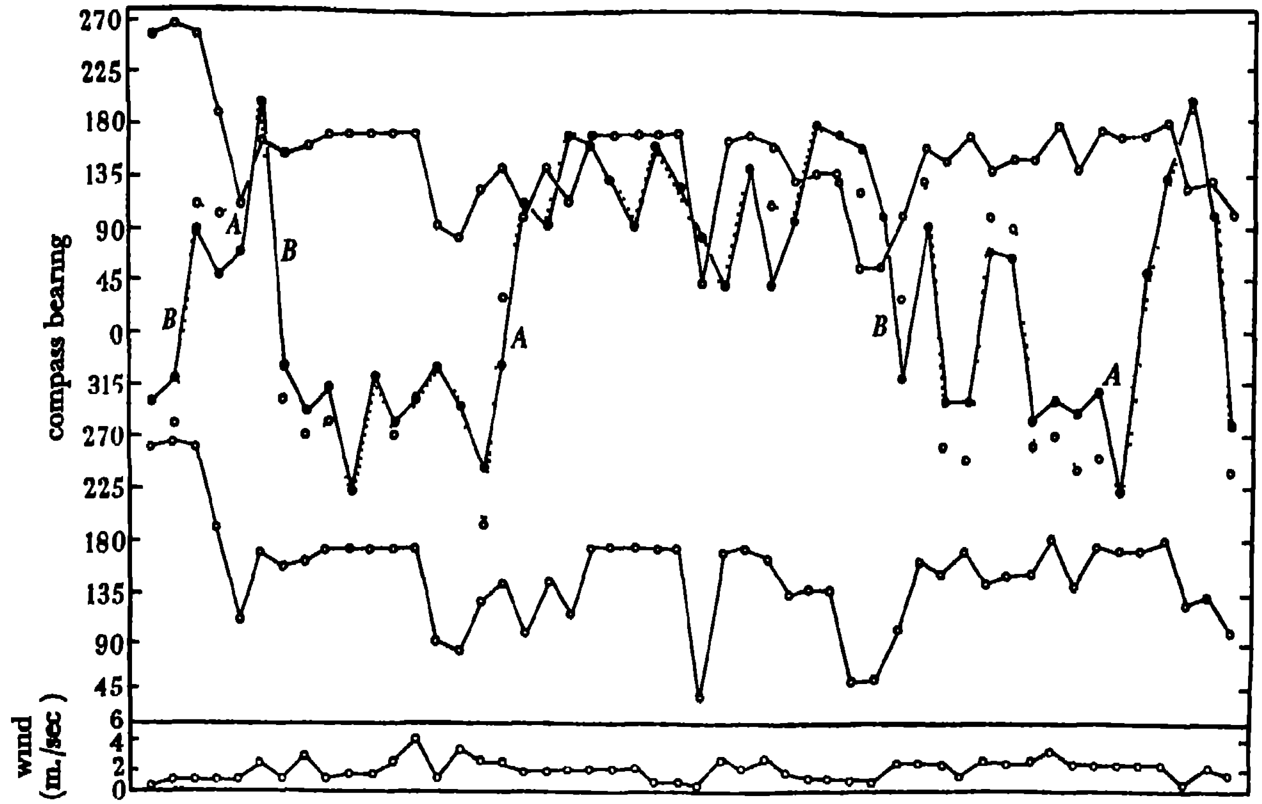

Figure 10 Individual direction readings from fledgling locusts flying 2 to 6 m above trees, with periods of roughly up-wind flying alternating with periods of down-wind flying Constructed as figures 8 and 9, but direction axis extended so that the wind direction (toward which it was blowing) appears twice, to make clear the relation between locust and wind directions — • —, course of locusts, o , track of locusts, — o —, wind

dropped, but most of the time the wind speed was over 2 m /sec and the great majority of the locusts were grounded Those that took off then did so into wind, but were immediately deviated on to cross-wind tracks and reoriented themselves accordingly, as described on

p. 184, in such a way that backward drift was as a rule prevented It was from these disoriented individuals that the readings were taken, which did not therefore represent level, steady courses and tracks Very few of these individuals managed to hold even an approximately up-wind course (*P*), and some turned nearly (*Q*) or completely (*R*) round on to a down-wind course These flights were all brief, for the fliers soon came down and reoriented into wind close to the ground or settled again

The behaviour of fledglings not in a position to reach the ground so quickly, because they were higher up when the wind became too strong for them, was recorded on 12 June 1943 (figure 10) The recorded fliers were at 2 to 6 m above the trees of an oasis The tracks of lower fliers (not recorded), in calmer air, seldom diverged from their courses which were slightly to the left of due up-wind But the tracks of the higher fliers, exposed to stronger winds, frequently diverged from their courses For varying periods, nearly all the higher fliers would be facing and flying roughly up-wind like the lower fliers, but then they began to waver, their tracks diverged from their courses and they then turned right round and flew roughly down-wind The more frequent occurrence of down-wind courses and tracks among these fliers, than among those closer to the ground at the same time or those recorded in figure 9, seemed to be due directly to their greater distance from the ground They were exposed to stronger winds and, taking longer to come down and settle, they were exposed for longer to winds against which they could not make steady headway, so that the reorientation response received fuller expression In figure 10, it will be seen that the readings fall into two groups, either roughly up-wind or roughly down-wind, with switching from up- to down-wind (*AA*) and vice versa (*BB*) The switchings are not obviously correlated with changes in the wind speed in the figure, for the anemometer was below the level of the locusts and somewhat sheltered by trees The wind-speed changes to which the high-fliers were exposed could often be inferred from the waving of foliage and the momentary quickening or slowing of the fliers' ground speed, and it appeared that switches from up- to down-wind followed sharp gusts and switches from down- to up-wind occurred in lulls However, the occurrence or non-occurrence of such a switch appeared to depend not only on wind-speed changes, but also on the density of the fliers (gregariousness, see p 194)

We may now consider the records of flight direction in relation to wind, collected from all the swarms observed Numerically, these constitute more substantial evidence than any so far quoted, but are given last because they are not direct evidence of the wind *responses* discussed above If, however, such responses are real and important, then we might expect them to be reflected in the frequencies at which different courses and tracks appear at different heights and wind speeds

The predominant relation between flight direction (course) and wind direction on each occasion when full migrants were seen has been taken from table 2 and entered in table 6 according to the height of flight and the wind speed prevailing near the ground (at 1 5 m) There were a total of forty-six occasions when both wind and swarm had a definite direction The bottom line of table 6 shows that, among these, the swarms were flying roughly up-wind on thirty and down-wind on nine occasions Flights at 45 to 90° from due down-wind occurred on three and at 90 to 135° on four occasions

In the main body of the table, where the observations are classified by height of flight, the totals are smaller because not all the swarms extended both above and below 8 m The number of down-wind flights below 8 m was equal to the number over 8 m (seven swarms extending to both levels) The number of up-wind flights below 8 m was, however, nearly twice the number over 8 m (eleven swarms extending to both levels) At both heights all but one of the eight cases of down-wind flight occurred with winds at 4 or more m /sec , and

TABLE 6 COURSES OF FLIGHT IN RELATION TO WIND DIRECTION, ACCORDING TO GROUND WIND SPEED AND HEIGHT FULL MIGRANTS ONLY DATA FOR PREDOMINANT BEHAVIOUR, FROM TABLE 2

height of flight (m)	wind speed (m /sec)	frequency distribution by angle from due down-wind (0°) (actual numbers)				totals
		0–45	45–90	90–135	135–180	
<8	<1	0	2	2	1	5
	1–<4	1	0	2	21	24
	4+	7	0	1	5	13
	total	8	2	5	27	42
>8	<1	0	2	0	2	4
	1–<4	1	0	1	12	14
	4+	7	0	0	0	7
	total	8	2	1	14	25
total swarms		9	3	4	30	46

TABLE 7 COURSES AND TRACKS OF FLIGHT IN RELATION TO WIND DIRECTION, ACCORDING TO GROUND WIND SPEED AND HEIGHT FULL MIGRANTS ONLY AMPLIFIED DATA INCLUDING FREQUENTLY OCCURRING AS WELL AS PREDOMINANT BEHAVIOUR

height of flight (m)	wind speed (m /sec)	course or track	frequency distribution % by angle from due down-wind (0°)				no obs
			0–45	45–90	90–135	135–180	
<8	<1	C	4	22	22	52	23
		T	4	22	22	52	
	1–<4	C	6	9	13	72	46
		T	14	17	15	54	
	4–7	C	28	18	23	31	39
		T	52	15	13	20	
>8	<1	C	8	25	21	46	24
		T	8	25	21	46	
	1–<4	C	12	16	12	60	25
		T	20	28	12	40	
	4–7	C	57	15	14	14	14
		T	72	10	9	9	

five of these cases occurred during winds of gale strength (nos 6–10, table 2) At both heights the majority of up-wind flights occurred in winds of 1 to <4 m /sec , but while there were five up-wind cases in stronger winds below 8 m , there were no up-wind cases in such winds above 8 m

The total number of cases is small if only predominant directions are taken into account as above These are therefore supplemented, in table 7, by a selection of the 'snapshot' readings taken during the more extended observations on single swarms Many of the readings obtained during such detailed studies represented temporary conditions diverging more or less from the predominant one at the time Although only the predominant direction represented the effective direction of migration at the time, the supplementary data can be used legitimately for the study of behaviour Only those relations between wind and flight which occurred especially frequently among the assortment of relations noted during any one swarm study have been selected for inclusion, together with the predominant relations at the same time, in table 7 The same figures are presented graphically in figure 11. Figures for semi-migrants, arrived at in the same way, are presented in table 8 and figure 12

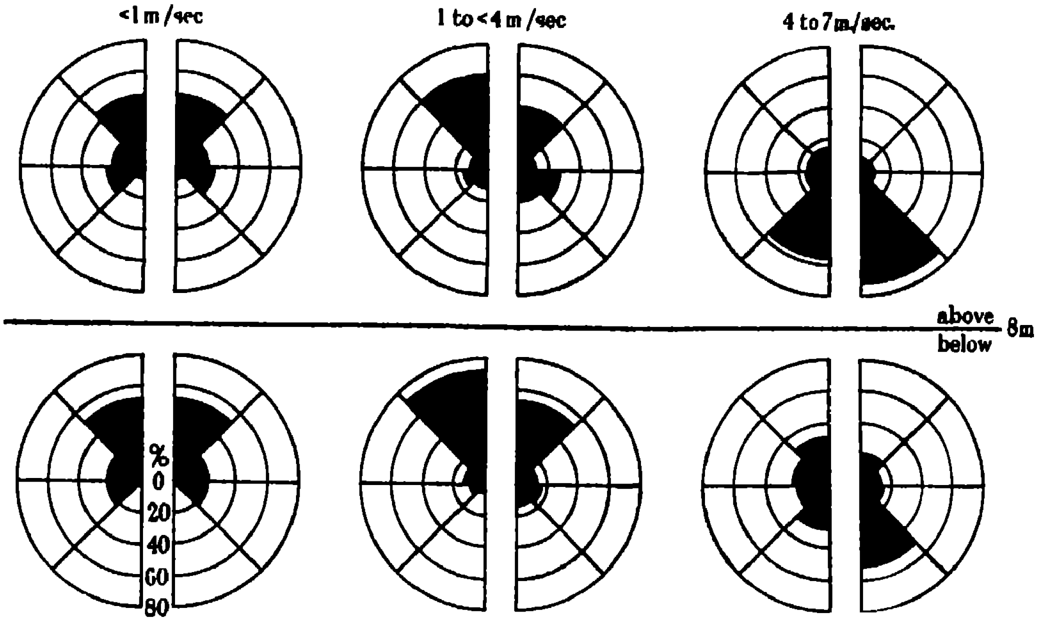

FIGURE 11 Frequency distributions of observed directions of flight of fully migrant locusts, according to height and wind speed Wind is assumed to be blowing from the top of the page Locust courses are shown in the left half, and tracks in the right half of each of the six diagrams Each half diagram is divided into four sectors representing courses or tracks deviating by 0 to 45, 45 to 90, 90 to 135 and 135 to 180°, from due up-wind Deviations of course to both left and right are shown together as deviations to the left, and deviations of track to both left and right are shown together as deviations to the right, the particular side toward which the deviations occurred being immaterial here Within each of the four sectors a portion is blacked-in with a radius equal (on the scale shown in the bottom left diagram) to the percentage of records within that range of deviations Data from table 7

TABLE 8 COURSES AND TRACKS OF FLIGHT IN RELATION TO WIND DIRECTION, ACCORDING TO GROUND WIND SPEED AND HEIGHT SEMI-MIGRANTS AMPLIFIED DATA INCLUDING PREDOMINANT AND FREQUENTLY OCCURRING BEHAVIOUR

height of flight (m)	wind speed (m/sec)	course or track	frequency distribution % by angle from due down-wind (0°)				no obs
			0–45	45–90	90–135	135–180	
<8	<1	C	19	19	12	50	16
		T	19	19	12	50	
	1–<4	C	28	19	17	36	59
		T	34	22	15	29	
>8	<2	C	31	23	15	31	13
		T	31	23	23	23	

For what they are worth, the figures clearly fit the conclusions drawn from the continuous observations of single swarms The reversal from preponderantly up-wind to preponderantly down-wind orientations, when the wind exceeds 4 m/sec, reflects the direct observations of such reversal occurring when the locusts ceased to make direct headway against such winds The figures bring out a further point, that across-wind orientations were rare except in light winds The lower proportion of up-wind courses among higher than among lower fliers, reflects the direct observation of the lesser responsiveness of higher fliers In winds of 4 or more m /sec there is a lower proportion of down-wind courses among lower than among higher fliers, which reflects the direct observation that the response of turning down-wind, although not so readily initiated among higher fliers, was nevertheless more often carried to completion and the new orientation maintained than among lower fliers which were able to settle or resumed up-wind flight instead

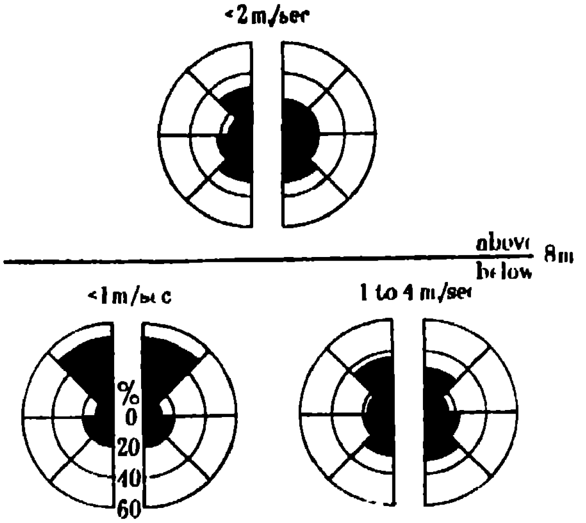

FIGURE 12 Frequency distributions of observed directions of flight among semi-migrant locusts, according to height and wind speed Constructed as figure 10 Data from table 8

The numerical data for semi-migrants (figure 12) present a picture similar to that for full migrants, except that the change-over from up-wind to down-wind orientation occurs at a lower wind speed, corresponding with the observed weakness of the flight of semi-migrants

To sum up, the body orientation of low-fliers was across the wind (90 ± 45°) in only a minority of cases The minority was considerable, but it was smaller in moderate than in light winds In the majority of cases the orientation was against the wind, or with it when the wind became too strong, and the wind strength which was too great depended on whether the locusts were full migrants or not But once again it is very desirable that more and more precise data be obtained on these questions

Behaviour over water The effect of wind on swarms flying over water was observed twice, on 23 and 24 May 1944, at Lake Naivasha, Kenya These observations are treated separately here because behaviour over water differed from behaviour over land in material respects The behaviour of part of the swarm observed on 24 April 1944 has already been described, that part which had already left the lake and passed on over the shore and came down when the wind speed increased The remarkable point was that the part of the swarm that was still over the water when the wind strengthened, did not come lower The same applied to higher flying locusts that had advanced only a little distance over the land when the wind increased, and were blown back over the water before they had time to drop down among the trees These two sets of locusts remained at the same height and were carried down-wind although still facing up-wind, while their fellows over the land had not lost ground but dropped low among the trees

The same effect was observed on the previous day when a large pink swarm made repeated sorties from the northern shore of the western arm of the lake, heading south against the wind The swarm was observed through field-glasses from the opposite shore The following sequence of events was repeated five times At the end of a spell of strong wind, 5 to 8 m /sec (as recorded on open, raised ground), the locusts had disappeared from view on the land, where they had settled or were flying too low to be seen The wind speed then dropped to 2 to 5 m /sec , and in a minute or two the locusts rose into view, flying steadily against the wind and in increasing number, and moved out over the lake Over the land they remained relatively low, not exceeding 15 or at most 30 m , but as they advanced over the water they deployed upwards to 100 or more metres Sometimes they advanced as much as 1 km over the water in this way, sometimes much less, before the wind rose again and drove them back Each time this happened they drifted back in disorder and without losing height as long as they were over the water, in contrast with swarms driven back by gusts over land which soon regained their cohesion by turning *en masse* down-wind, and came lower As soon as the lake swarms reached the land, however, they became more orderly, began to lose height rapidly and, if the wind did not drop in a few minutes, they all dropped down out of sight

These were the only occasions when locusts were seen to offer no resistance to being carried backwards by the wind On both occasions they were over a considerable sheet of water, which suggests that the failure of the normal behaviour was due to the uniformity of the visual field below

Gregariousness

The term *gregariousness* is used here in the strictly behavioural sense, meaning the tendency of swarm members to act in certain ways because other locusts are doing so and not because all are responding to a separate, common source of stimulation

Flight activity The flight-engendering effect of mutual stimulation was evident during the process of increasing flight activity culminating in mass departure, as already described From the start of *milling* onwards it was noticeable that taking-off was flaring up and dying down again among whole groups of locusts, now at one series of points and again in a different series of points in the swarm Taking-off, started by a few individuals, would run through the cluster along a tree branch like a flame Meanwhile neighbouring clusters remained perfectly quiet, until for some reason a few of their members took off, and the activity spread through fresh masses of insects Groups of flying locusts flushed up resting ones from trees and from the ground *Milling* passed into *surging* as the groups enlarged, gregariousness and rising temperature apparently collaborating in bringing more and more insects into the air together

The flushing up of settled locusts by flying ones passing over them reached a climax in the mass departure of the swarm Up to mass departure there were still large numbers of settled locusts beside those flying Within quite a short time—15 min or so in our observations (figure 1)—they were all in the air, having risen in a succession of clouds from this point and that, as their fellows swept over them with the setting in of uninterrupted flying

However, it was always noticed that the locusts which took off early, when flights covered only a few metres, did so individually, without appearing to affect their neighbours (cp Gunn *et al*, 1948, p 14) Moreover, the trickling departures of semi-migrant mating and laying swarms consisted of innumerable takings to flight by individuals, again not apparently stimulated by their neighbours And later in the day, when swarms were migrating, full migrants were often seen flying alone In Iran, in May 1943, migrants were seen in very loose flights or as completely isolated individuals more often than they were seen in coherent swarms Individual migration was also seen in Kenya in 1944, although less frequently It was not known whether these migrants were already isolated when they started flying, or started in a swarm and became isolated later

Thus although mutual stimulation appears to contribute to flight activity, both taking off and sustained flight can occur when mutual stimulation is relatively weak or even absent

Flight direction The term *gregarious inertia* has been applied to the tendency of a locust hopper band to continue moving in a straight line, thanks to the responses of hopper to hopper (Kennedy 1945) This effect was evident also in flying swarms, and most strikingly so when two columns of locusts met at an angle, as observed among maturing locusts in Kenya and several times among fledglings in Iran The result has been described by Zolotarevsky (1929, 1930), the locusts from one swarm change their direction to that of the other according to which swarm is the denser at that point and time

The case observed in Kenya, at Nakuru, on 31 March 1944 was a variant on Zolotarevsky's Column *A* was flying east and denser in its upper layers than below, when it met column *B*, which was flying at the same height and was as deep as *A*, but was flying south-east and denser below than above At the point of mixture most fliers in the upper part of *B* joined column *A*, whereas most in the lower part of *A* joined *B* Where the columns were denser, in the upper part of *A* and the lower part of *B*, the locusts remained largely undeflected Cases of locusts reorienting each other in this way attract most attention when they occur in full flight, but exactly the same thing can be seen again and again in a swarm surging about prior to the mass departure from the night roosting site Indeed, the mass behaviour pattern leading up to the mass departure of swarms in the morning is one long display of direction changes mediated by gregariousness, or *gregarious re-alinement* The essential principle of gregarious re-alinement remains the same throughout the process What changes progressively is the number of insects involved in each re-alinement manoeuvre The roles of provoker and executor of a gregarious re-alinement are filled at first by single insects, and then by ever-growing groups of them together until finally there is only one group, the whole swarm at mass departure

Gregarious re-alinement was also seen in swarms in the course of migration during the day, under the influence of wind, and the difference between loose and dense swarms in this respect provided additional evidence of the role of gregariousness in regulating flight direction The effects of wind, described in the previous section, were essentially similar in loose and dense swarms But when the locusts were dense, their responses were more definite and less ragged than when they were thin Dense locusts seemed less easily driven back and deflected As long as the majority managed to make headway, deflected individuals came back into line quickly On the other hand, as soon as a considerable proportion of the individuals began to be deflected and so to turn, the whole part or layer of the swarm reversed its direction with remarkable rapidity This phenomenon had a clear gregarious component It was noticed in both migrants and fledglings, more often in the latter (e g figure 10), because the customary moderate wind was able to initiate a down-wind turn in these feeble fliers more readily than in migrants proper

The following impression was formed of what happened during gregarious reversal A mass of individuals was flying against the wind, which then increased in strength Some individuals began to lose ground and turn away from their up-wind course In consequence they began immediately to drop backwards relatively to their fellows The immediate neighbours responded to this relative displacement by themselves turning and pursuing the deflected individuals, so that the neighbours assumed a due down-wind course even sooner than the initially deflected locusts The result was to accelerate and fix a due down-wind course throughout the swarm whenever it became difficult for many individuals to make headway directly against the wind, but before it had become impossible for them all to do so

The return of dense low-fliers to an up-wind orientation when the wind dropped again was seen to be accelerated in the same manner As soon as a number of individuals had regained their up-wind course the others quickly followed suit In the upper layer of loose swarms the reversal from up- to down-wind orientation was relatively slow and ragged Where higher fliers were dense, and hit by a wind gust, the temporary confusion was more marked than among low-fliers, but then the rapid, unanimous reversal to down-wind was at least as conspicuous as in dense low-fliers Mass reversal of higher fliers (>8 m) was also observed when low-fliers were maintaining their up-wind course and managing to make some headway Thus gregarious reversal is merely a special case of direction changes mediated by gregariousness, or gregarious re-alinement, in circumstances where all except two, opposite directions are excluded by another factor, wind *

Despite the above observations suggesting that gregariousness participates in direction determination, it should be emphasized that mutual stimulation is not essential for steady uni-directional and parallel movement by a large number of individuals In Iran on 20 May 1943, for example, the average density of a passing swarm was estimated as one individual every 10 m , and some individuals were hundreds of metres from their nearest fellows Yet all the individuals were flying steadily on the same course Also, during the departure of both fully migrant and semi-migrant swarms, the assumption of a common flight direction was observed to occur among individuals completely cut off, at least visually, from their fellows (p 172)

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* Gregarious reversal can be seen in swarms of other insects The writer observed it, for example, in a large swarm of male Chironomids stretching 10 m along the centre of a narrow road bounded by high hedges near Salisbury, Wiltshire, in 1945 The midges were dancing 2 to 5 m above the road surface, directing themselves into the light air drift along the road Whenever the wind freshened, two things happened The whole swarm shifted to a lower, more sheltered level, and mass down-wind turns occurred wherever the midges began to be carried backwards over the ground At times a fast-moving *wave* of gregarious reversal was seen to pass back along the swarm, as down-wind fliers passed successive lots of the other midges, till then still facing up-wind and keeping their position with reference to the ground, but which now joined the down-wind surge The down-wind movement occurred most commonly in the upper, more exposed layers of the swarm, producing the situation often seen among locusts and butterflies, the upper layers of the swarm oriented down-wind and the lower layers oriented up-wind As soon as the wind dropped again, all the midges soon resumed their up-wind orientation, moved higher into the air and kept their rough position with reference to the ground despite moments of chaos caused by passing vehicles or the human voice

tial minority hesitated and turned away momentarily when over or near the cloth, resuming their previous course as they passed away Four individuals suddenly changed course when over the cloth, came down and settled on the gravel within 3 m of it Twelve others did not change course, but came down and settled on the gravel within 15 m of the cloth after passing over it None of the hundreds that passed over the cloth above 3 m descended, but about twelve flying at 5 to 10 m came down and settled 3 to 5 m *short* of the cloth The fact that higher fliers responded before passing over the cloth but lower fliers afterwards, is contributory evidence that the response was visual, for the higher fliers would see the cloth sooner than lower fliers

The cloth was spread again later on that day, but locusts were fewer and flying rather higher, while the background was less suitable It was a light sandy patch in a dry river bed, but nearby and along the locusts' flight route there were many patches of contrastingly darker ground, and the sun was obscured No responses to the cloth were noted

The black cloth was spread a third time, together with a red one, on open, light-coloured ground on 13 June 1943 During 30 min about five hundred locusts crossed each cloth within about 3 m above it, and many more at greater heights This time there was a certain amount of spontaneous settling, for nineteen low-fliers came down and settled elsewhere in the vicinity nowhere near a cloth But no sudden changes of direction occurred elsewhere in the vicinity, whereas many fliers hesitated on passing over the cloth, veered away, resumed their original course and flew on Perhaps fewer locusts were caused actually to settle by the cloth on these second and third occasions because the locusts had been flying already over a variety of backgrounds In the first exposure of the cloth the locusts had had no such distraction for perhaps hours *en route*, and the black patch must have been a very novel feature in the landscape for them

The results of these trials showed that migrants could not be caused to settle in appreciable numbers by a black conspicuous object More interesting, however, was the fact that many did react to it as they passed over by hesitation and change of direction, soon corrected Settling appeared to be merely an extreme form of the reaction to the same kind of stimulus

The question naturally arises as to whether such effects occur also on a much larger scale when their importance would be correspondingly greater Unfortunately, it is impossible to distinguish the visual effects of large-scale physical features from the other effects of such features, such as changes in wind, temperature, etc , but one or two field observations may be mentioned here

Near Bandar Abbas, Iran, on 27 April 1943, a large, loose, pink swarm extending from the ground up to about 50 m was 'rolling' in little wind across the level floor of a wide valley In front of it was a steep-sided ridge 150 m high On coming up against this wall many fliers settled at its foot, but others turned and flew along it until they drew level with a gap where the ridge was only 50 m high, whereupon they turned into their old direction and streamed through the gap

Direction changes in face of a change in the visual field, but without any solid obstacle in the way, were observed among Desert Locust swarms reaching the coast of Algeria in June 1944 (personal communication from Mr G F Burnett) A swarm was observed traversing the coastal plain near Reghaia, about 25 km east of Algiers, on 16 April 1944 The locusts flew north-north-east toward the sea, across a light westerly wind, and extended from the ground up to about 100 m On reaching the shore-line the leading locusts turned back into the main body General confusion resulted, but out of it a new direction of flight emerged, now along the shore-line to the west-north-west On the 21st a second, larger swarm appeared flying northwards On reaching the shore-line the locusts again did not cross it but drifted along it, now in one direction and now in the other In these cases there may, of course, have been a change in the condition of the air at the shore-line, and the locusts' change of direction was not necessarily due to the sight of that line But here again, the comparable behaviour of marching hoppers (Kennedy 1945) when stimuli other than visual ones could more safely be ruled out lends some support to the view that the adults were reacting mainly visually

The opposite of obstacle-avoidance, that is, *attraction* to conspicuous objects, was also observed, but not among migrants in full flight For example, fledglings were observed for some days in June 1943, in and around the luxuriant oases (walled gardens) or tamarisk groves, both surrounded by arid wastes, in the district south of Bam on the edge of the Dasht-i-Lut (south-east Iran) Hoppers had developed all over the area The fledgling adults did not migrate *en masse* for a week at least, but every day they flew in loose flights for short periods, frequently brought down by the wind and never progressing far In the course of these flights they collected in large numbers in the oases Once they reached an oasis they may have been held there by a number of features such as food, shelter from the wind and the noticeably lower temperature and higher humidity, but it was obvious from direct observations that they were also held by visual attraction to the conspicuous trees and buildings When they took to the air they were often carried out on to the bare ground, but rapidly flew back to the oasis even if this meant unusual exertions for them in flying against the wind Since the return to the oasis or tamarisk grove was also made across or even downwind, it could not be attributed then at any rate to any wind-borne moisture or odour The attraction was most evident toward evening when the locusts abandoned the open ground altogether and collected in the oases or on any trees, even isolated ones, outside it

Again, clumps of trees, the most conspicuous feature of the immediate landscape, were pointed out to us by farmers in Kenya as the habitual roosting sites of any swarms that settled in the locality The locusts either settled directly on these clumps as migration slackened toward evening, or they settled in the fields and later flew up into the trees before nightfall Of settled swarms observed by us, all were crowded on the tallest vegetation available If that consisted of only a few shrubs and small trees these were heavily laden with locusts, with the rest of the swarm less thick on the ground One swarm was found settled at Morendat, Kenya, on 22 April 1944, in park-like country with irregularly spaced trees of various sizes, and the locusts had gathered almost exclusively on the upper parts of the tallest of them

REVIEW AND ANALYSIS

Influences affecting swarm behaviour

The condition of the locusts

The fact that full migratory flying does not appear immediately after the final moult, but develops gradually, was made clear by Uvarov in his book (1928, see also Predtechensky 1935*b*, Khan 1945, Johnston & Buxton 1949) Further aspects of this process, brought out here (pp. 173–175), are that the hardening of the cuticle is not complete even when the young locusts have started persistent mass flying, and that, associated with the softness of the body perceptible for a number of days after the last moult, there is a lack of power in flight, reflected in the inability of fledglings to make headway against weaker winds than fully hardened locusts In this way fledglings develop the habit of persistent flight before they are strong enough to resist carriage by the wind as well as older migrants do, which is likely to make a considerable difference to the large-scale, *resultant* effects of their migratory activity (Part II)

The reduction of migratory activity around the time of mating and egg-laying, observed during the present studies, was also indicated by Uvarov (1928), who wrote that a period of 'daily circular flights without any definite direction' preceded oviposition The reduction in migration is not apparently due to direct preoccupation of the insects with reproductive activity, for in any swarm seen mating and laying there are many individuals not participating in these activities but yet not migrating In addition to the direct loss of flying time through engaging instead on mating, laying and associated activities, there seems to be a reduction in the effort put into such flying as is done (pp 175 and 192) In this respect sexually active locusts come to resemble fledgling locusts, in their resultant behaviour with respect to wind, so that locusts in these two conditions have been classed together as *semi-migrants* (p 173) But the reduced migratory activity of sexually active locusts is not due to physical weakness, as in fledglings (pp 173–177), and must be attributed to some transient physiological inhibition Whatever the internal cause may be, it has the effect of permitting reproductive activity to develop fully without interference from the locomotory activity which preoccupies the insects so strikingly all the rest of their lives

It has been suggested that sexual maturation affects migration not only incidentally, in the way just mentioned, but quite fundamentally, being its real cause Uvarov (1928, p 86) wrote

> ' physiological factors, which must be considered the real cause of flight There can be no doubt that the emigration flight is intimately connected with the process of development of the genital products An internal stimulus for the flight during the maturation of genital products is prevalent in other insects, such as termites and ants, in which a so-called nuptial flight precedes copulation, this is exactly what happens in locusts '

This idea has found no place in Uvarov's subsequent writings, but deserves mention because it has been widely accepted, for instance by Imms (1937, p 306), although it will not bear examination in the light of the facts

In undertaking migration, adults are merely resuming an activity which is no less characteristic of the same insects as hoppers Adults employ a more spectacular form of locomotion, flight, when migrating, than do the hoppers which can only walk or hop But the behaviour of adult gregarious locusts is recognizable as migratory because of the extraordinary *persistency* of their locomotion, not because of its particular form The locomotory activity of hoppers is no less persistent, being interrupted only by moulting, given favourable conditions Adults resume migration while they are yet fledglings and continue to migrate, with interruptions, when their sexual organs and behaviour are fully developed, even until they die (p 175 and Waloff 1946*a*, p 63) In the normal course of events gregarious Desert Locusts grow, live and die as migrants Migration is thus a fundamental property of the insects, not connected with any particular stage of their physiological development

Wind

General Wind is probably the most frequently cited of all possible influences upon adult locust migration, and yet is the one over which there is least agreement

It will be seen in later sections that the behaviour of migrant adults resembles that of hoppers in many ways Since hoppers, being earth-bound, are easier to study, it is often possible to use hopper observations as pointers for the analysis of adult behaviour That is done in this paper, for the ultimate aim here is to distinguish what is essential from what is derivative in the behaviour of migrants, whether they be hoppers or adults If adult migration has usually been considered by itself, apart from hopper migration, it is the role of the wind in adult behaviour which must be held mainly responsible, for it has seemed as puzzling as it was obviously important Adults fly they leave the hoppers' fixed substrate, the earth, and move in a medium, the air, which itself moves in a complicated manner This could hardly fail to impose a new resultant pattern on their behaviour even if in essentials it were the same as that of hoppers Hence, as a necessary step toward distinguishing those essentials, attention was concentrated on the role of the wind in the present studies on adults

The evidence we have concerns the effects of wind on the speed, height, frequency and direction of flight

Some impressionistic evidence is available that low fliers regulate their air speed according to the wind speed (p 177) If this were confirmed, estimates of the air speed of low-flying locusts would vary with the wind speed No general validity could then be attached to the figure of 15 ft /sec (4 6 m /sec) recorded by Mr J F Graham in Kenya in 1946, although this was quoted by Gunn *et al* (1948, p 45) as the 'first measurement of air speed made by a rigorous method' Mr Graham kept pace with a locust while carrying an anemometer and so obtained the true value of that locust's air speed at that moment But the very rigour of his method, excluding as it did the wind speed from measurement and therefore from attention, restricts the value of his result *

The following estimates have been published of the flying speed of Desert Locusts explicitly stated to be in calm air near the ground 3 1 m /sec (Hall 1840), 4 2 m /sec. (de Lépiney 1928), 2 7 m /sec (Cheesman 1929), 2 7 m /sec (Williams 1933), and 8 0 m /sec (Rungs 1945) Apart from Rungs's exceptionally high figure, these estimates of locust air speeds, under conditions when these were also ground speeds, are rather strikingly alike Observers in Algeria (1929) gave similar figures, 2 8 to 4 2 m /sec , for the 'normal' speeds (presumably *ground* speeds) of swarms under unspecified wind conditions and at unstated heights, while a similar range of *air* speeds, 2 5 to 4 m /sec , is given here (p 177) for locusts flying low against light winds Mr Graham's figure of 4 6 m /sec in unknown wind approaches the mean figure of 4 9 m /sec in a variety of conditions given by Rainey & Waloff (1948) Perhaps these higher figures were due to the locusts increasing their air speed against head-winds, and an observation of Gunn *et al* (1948, p 45) is noteworthy in this connexion A swarm was observed flying low, at a ground speed of about

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* Also, the speed of Mr Graham's locust may have been influenced by his very pursuit of it

1 8 m /sec, although opposed by a wind of about 4·6 m /sec It must therefore have been maintaining an air speed of more than 6 m /sec Waloff & Rainey (1951) found that the calculated, instantaneous air speeds of a number of Desert Locusts flying at 3 to 12 m above the ground (see p 205), varied little, despite wide variations of wind speed This leaves the question open, for it was only locusts flying closer to the ground which gave the impression, to the writer, of adjusting their air speed in relation to short-term changes of wind speed (p 177) Further observations are needed both in the field and in the laboratory to see how far locusts do in fact regulate their ground speed in the way suggested

The inverse relation between wind strength on the one hand and the height and frequency of flight on the other (p 178) has often been referred to in the literature by Koeppen (1870 *Locusta*), Kunckel d'Herculais (quoted by de Lépiney, 1928, 1933 *Schistocerca*), Regnier (1931 *Schistocerca*), Zimin (1934 *Calliptamus*) and Zolotarevsky (1929 *Locusta*), and the present observations provide some quantitative evidence on the point

It is over the relation between flight *directions* and the wind that there has been the most confusion in the literature Among those who have made direct observations on a number of swarms in full flight, Ballard, Mistikawi & Zoheiry (1932 *Schistocerca*), Lean (1936 *Locusta*) and Gunn *et al* (1948 *Schistocerca*) have described a preference for down-wind flight Synoptic studies, that is, the mapping and analysis of all available locust reports in relation to the meteorological records, such as Lean's (1931 *a*) analysis of the great outbreak of *Locusta migratoria migratorioides* during 1928–31, Waloff's (1946*a*) analysis of the movements of *Schistocerca* in East Africa, and Rainey & Waloff's (1948) study of Desert Locust swarm movements and air-mass trajectories over the Gulf of Aden, have shown general agreement between migration direction and wind direction (with-wind migration) On the other hand, Lean's (1931 *b*) more detailed studies in Nigeria did not show such consistency, major movements being sometimes obliquely up-wind, sometimes directly up-wind and sometime down-wind, and he believed humidity was the key factor In his review of the annual cycle of solitary and gregarious *Schistocerca* in India, Rao (1942) points out that the two major migration trends, that eastwards from the spring breeding areas and that westwards from the monsoon breeding areas, appear to be due to winds in those directions

Many authors have contented themselves with stating general conclusions or impressions or describing isolated cases, and by these down-wind flight is again most frequently stressed (e g Lallemant 1865, Vosseler 1905, Andrews 1915, Vrydagh 1932, Bruzzone 1936)

There are a number of accounts of swarms flying with the wind in front of storms For example, the following appears in an unpublished note by C L Collenette

> 'On 23rd September, 1929, a large swarm passed over Buran (British Somaliland), flying south, exactly before the wind, which was moderately strong The main body was perhaps 500 ft up, and made much noise From the direction from which they came, rain clouds and rain could be seen, but this did not reach Buran.'

In the same country and year, Farquharson (1930) described a succession of enormous swarms migrating southwards at great height immediately in advance of heavy rain A reliable observer, living near Eldama Ravine with a commanding view over the Kamasia Reserve toward Lake Baringo, Kenya, informed me he had often watched swarms flying southwards against the prevailing wind, in 1944 and previous years Time and again, he reported, a swarm would fly slowly but steadily on up the slopes in the sun until met by a rainstorm blowing up from the south Thereupon the swarm was thrown into confusion for a few minutes and a new, reversed direction of flight emerged, the swarm now flying fast with the wind back to the sunny lowlands, whence it returned later, flying slowly up-wind again

Even among authors giving only general conclusions or quoting isolated cases there are several who stress up-wind flight (v Frauenfeld 1870, Faure 1894, Siyazov 1928, Cheesman 1929, Zolotarevsky 1929, Allan 1933, Predtechensky 1935*a*) It is among the longer-range movements that down-wind movement is most apparent, but at least one major migration trend by *Schistocerca* is against the prevailing wind the northward movement in spring in North Africa, Arabia, Iran and Baluchistan Waloff (1946*a*, p 50) found evidence of a tendency for old mature swarms to move against the prevailing wind in East Africa even when younger swarms were not doing so Key (1942) found a definite up-prevailing-wind preponderance among numerous records of *Chortoicetes terminifera* swarms

Finally, every field observer has seen swarms flying neither against nor with the wind, but across it, or in so little wind as to make it virtually inconceivable that it was exerting any directing influence, while yet the locusts showed at least as much unanimity and stability of orientation as they do when flying against or with the wind

In seeking to bring some order into this confused field, authors have adopted very different approaches Fraenkel (1932), reviewing the subject of insect migration at a time when much less information was available on locusts than to-day, concluded that they were often carried on the wind but did not actively orient to it To-day, however, our fuller information on locusts presents a superficially confused picture similar to that Fraenkel then described for butterflies Yet, while recognizing the lack of any fixed relation between migrant butterfly directions and wind directions, Fraenkel insisted that this did not exclude the possibility of causal role for the wind in many of the cases when with- or against-wind migration was reported, and he discussed means by which flying insects might orient actively on the wind (see below)

Waloff (1946*b*) and Rainey & Waloff (1948), on the other hand, chose for analysis some rapid, long-distance swarm movements made when 'the wind speed is greater than the air speed of the locusts' so that the 'down-wind displacement would in fact occur even in the complete absence of any persistent orientation', and when the locusts were crossing the sea and so presumed to be obliged to remain air-borne This approach undoubtedly simplifies the situation, thereby enabling the meteorological aspects of a certain type of resultant displacement to be worked out, but it should not lead us away from the biological aspects of migration

Williams (1930, 1942, 1949) and de Lépiney (1928, 1933) do not merely leave on one side the orienting influence of the wind, they make out a case against it, except at the moment of taking off They draw particular attention to cases where the locusts' courses seem to be entirely independent of the wind De Lépiney stresses that the wind participates as a vector in determining the tracks of migrants, but believes their courses are independent of the wind Williams minimizes the wind's role not only as an orientator, but also as a transporter of the migrants Recognizing that a correlation between flight directions and prevailing wind directions often exists, he attributes it to chance, or to a 'psychological error' on the part of observers who unconsciously record flight directions as more accurately against or with the wind than they in fact are, or tend to classify them into only two categories, against or with the wind This tendency cannot be denied, and it means that the accumulated records of butterfly directions, for example, which show a clear preponderance of flights against or with the wind, are nevertheless unreliable evidence of any real preference for flight in those directions But if such records are valueless for the purpose of revealing a real preference strong enough to emerge from a mass of records taken under all sorts of conditions, they are equally valueless for the purpose of revealing something more probable a preference exercised in certain circumstances, but not in others Such records prove neither the presence nor the absence of active wind orientation

Both Williams and de Lépiney take the view that, since the direction of migration does not show a constant relation to the wind direction, some other environmental feature must be the real key to the orientation of migrants, and that therefore the wind's possible orienting influence can be disregarded As against that view, Kennedy (1948) and Gunn (1948*b*) have argued that the wind is one of many influences each of which is capable of determining orientation in some circumstances, but not in others, hence we need not seek some *one* environmental key to the orientation of migrants Gunn *et al* (1948), accepting the possibility that courses as well as tracks may be influenced by the wind, advanced the hypothesis of the 'forbidden course' (discussed below, p 222) However, the main conclusion they drew from their observations was that the diversity of flight direction—wind direction relations excluded at any rate 'some of the simplest hypotheses' concerning the wind's directing influence, such as that locusts always fly up-wind, or always down-wind Since it was that same conclusion which led Williams and de Lepiney to disregard wind altogether as an orienting influence, it cannot be too strongly emphasized that the diversity of flight-wind relations is entirely to be expected, considering that locusts fly in winds ranging in speed from well above to well below their own air speed Hence, so far from providing grounds for disregarding the wind's possible orienting influence, the diverse flight-wind relations demand closer analysis, before any conclusions can be drawn concerning that influence This point was made originally by Fraenkel (1932) when he wrote his review of insect migration

In embarking on the analysis we must revert, therefore, to the simple and fundamental, but neglected, point made by Uvarov (1928, p 86) that 'when there is no wind, or only a slight breeze, the flight is not affected, though strong winds always carry the swarms with them ' 'Always' is rather too strong a word, since the locusts often settle rather than let themselves be carried, but the fact remains that in strong winds, which exceed their own air speed, locusts must go with the wind if they fly at all Certain authors (d'Herculais quoted by de Lépiney 1928, Egypt 1916, Regnier 1926, Zolotarevsky 1929) have long gone further than this, noting the tendency of low-flying locusts to fly up-wind in light or moderate winds and to an increasing extent down-wind as the wind speed rises It has also been known for a long time that the orientation of flying locusts can vary according to their height above the ground, for Williams (1933), Predtechensky (1935*b*) and others have recorded instances like those cited here of swarms consisting of a lower layer of up-wind fliers and an upper layer of down-wind fliers

Such observations pointed the way for further work which would eventually lay bare the causal connexions between the wind and migratory behaviour But these pointers have not, in general, been followed up The data so far available have been collected without sufficient regard to the various circumstances which could have been expected, in the light of existing observations, to make important differences to the locusts' behaviour As a result, the collected data present a confusing picture and the only kind of generalization possible is a negative one, such as that of Gunn *et al* 1948 (mentioned above, p 204) or the following

'If in any district there is a prevailing wind, and also a more or less regular direction of migration, an apparent relation between wind direction and flight is bound to appear although it will be no evidence of cause and effect' (Williams 1942, p 233)

Williams went on to quote his observations on locusts which showed a preponderance of flights more or less against the wind 'But', he continued, 'as neither all possible flight directions nor all possible wind directions occurred one cannot draw any conclusion ' This statistical approach, which seeks mainly to increase the *quantitative* bulk of data, tends to lose sight of the qualitative diversity of such biological events, and to defeat its own end by postponing the drawing of conclusions until all possible flight directions and all possible wind directions shall have been recorded

The bewilderingly confused picture presented by the data published hitherto on flight direction in relation to the wind seems to be due, in other words, to the tendency to look for some fixed relation, unaffected by varying circumstances 'Ambiguous' observations, for example, of flight both up-wind and down-wind at the same time (above), have therefore been regarded as evidence against the wind having any important directing influence That in turn has meant inattention to the wind's speed, to the height of flight, to the courses as distinct from the tracks of fliers, to the condition of the locusts, and so on

A more systematic study of locust flight direction in relation to wind is that of Gunn *et al* (1948, p 45), who recorded all the above quantities except height of flight They observed predominantly down-wind tracks at all wind speeds down to about 1 2 m /sec , and against-wind orientations only at still lower wind speeds This appears to contradict my own findings of predominantly up-wind flight in winds up to nearly 4 m /sec , but their data refer solely to swarms that were just launching on migration in the morning and may not have attained their full, cruising air speed Gunn *et al* observations on swarms in full flight are fewer and are not accompanied by the circumstantial data necessary for comparative purposes

The most detailed contribution to this subject is by Waloff & Rainey (1951), who emphasize that behavioural preferences cannot be deduced from a series of observations on separate swarms A mobile observer can make contact with swarms flying slowly up-wind, more frequently than with swarms flying faster down-wind (cp part II, footnote on p 275), and the bias so introduced must not be mistaken for a preference of the insects It was for this reason that more importance was attached in the present account (pp 182–193) to variations of behaviour during continuous observations on single swarms, than to the collected records from all swarms The latter are regarded only as confirmatory, and that only after they have been classified according to criteria suggested by the continuous observations

Waloff & Rainey recorded the instantaneous courses and tracks of individual fliers, using a mirror 'flight direction-finder' (figure 7), with simultaneous readings of wind speed and direction, in the course of four periods spread over 4½ hr observation on a single

Desert Locust swarm The *mean* course of the locusts remained between 8 and 24° to the left of due up-wind during the first three periods, thereby following the progressive shift through about 40° which the wind underwent in that time A number of the individual courses were within 15° of due up-wind in all four periods, so long as the wind speed did not exceed about 3 m /sec But none were so close to due up-wind in stronger winds, and in the fourth period, when the wind was more gusty (exceeding 4 5 m /sec twice as often as it had before), the mean course deviated from the mean wind direction by 57° These findings are in general agreement with the present account, with the important addition of the evidence of locust courses changing with slow changes of wind direction Waloff & Rainey analyzed their individual records further, to see whether the effect of gusts was to cause the locusts to turn out of their up-wind orientation to the extent necessary to avoid backward drift, as suggested on p 184 They found no evidence of this, but 'snapshot' readings are not suitable for demonstrating the existence or non-existence of such a reaction, as emphasized on p 186 They take no account of the previous wind or previous behaviour of the locusts, in a situation where both are varying rapidly, both from moment to moment and between locust and locust A very large number of readings would be required to build up a connected picture of the fast-moving manoeuvres of any one individual in such winds Moreover, Waloff & Rainey's readings include locusts flying at all heights from 3 to 12 m That is a critical range of heights, to judge from the observations recorded in the present paper, so that aggregating the readings for analysis may have concealed some regularities

My own and others' observations which are quoted earlier (pp 182–193) were not made systematically or with the desirable degree of precision But attention, at least, was paid to all the circumstantial points mentioned above Considered together, the observations provide certain indications of an orderly system of flight direction–wind direction relations dependent on wind speed and height of flight These results, together with the findings on the effect of wind speed on flight activity and on the height of flight, make it worth while to consider how the wind may in fact affect the behaviour of the locusts, first as a direct mechanical stimulus to them and secondly as an indirect cause of visual stimulation

Reactions to direct stimulation by wind It is sometimes assumed (e g by Zolotarevsky 1929) that flying insects can sense the direction of the wind directly, by its pressure on their bodies, even if the wind be completely smooth This seems to be a misunderstanding, as Fraenkel (1932), de Lépiney (1933), Kennedy (1940) and Williams (1942) have pointed out Any object which exactly floats in air and which does not exert any propelling force tends to acquire quickly the velocity of the air In a completely smooth wind, once the velocity of the wind has been reached, such an object cannot have any wind force acting on it If the object is self-propelled then the only wind force acting upon it will be that due to its self-propulsion through the air Thus a locust flying in a smooth wind cannot receive any direct information about the wind speed or direction and cannot therefore react directly to it

If, on the other hand, the wind is not smooth but gusty, then at each gust an additional force, not due to its own propulsion, will act on the locust Williams (1942) discussing the problem of wind as a directing influence for migrant insects, has drawn attention to the work of Giblett (1932) on the structure of the wind Under adiabatic or superadiabatic air conditions, common during the day in clear weather, Giblett concluded (p 56).

> '. there are major eddies composed of alternating masses of fast and slow moving air, while embedded in the air masses there is a large number of small scale eddies These air masses are considerably longer in the direction of the wind than they are broad The changes of velocity in wind from air mass to air mass are characterised by abrupt increases and comparatively gradual decreases These facts have been found in eddies which are on the scale of 4000 ft long by 600 ft wide (these measurements are probably below the average) There is another group of major eddies which ranges up to a dimension in the direction of the wind of the order of 10–20 miles '

The major eddies, according to Giblett, show the same abrupt rise and slow fall in wind velocity, while the numerous, small-scale eddies are not elongated in the wind direction

The elongation of the air masses in the direction of the wind might provide an observer, who was himself being borne by the wind, with a clue as to its general direction As Williams (1942) says 'An insect would be subjected to a pressure from the direction from which the wind is blowing during the sudden advent of a gust, and a much weaker pressure on the opposite side as the gust dies away '

In order to respond to these forces, the insect would have to be equipped with suitable receptors which would record the fact that some part of its body was taking up the new wind speed more quickly than other parts The wings themselves could act in this way locusts observed being carried on a gusty gale sometimes had their wings blown forwards over their heads (p 183), the flat wings being more readily caught by the wind than the body (cp Williams 1930, p 384) But there was no evidence that these locusts were orienting to this unusual situation, for their orientation was the same as that of locusts flying in winds that were strong, but not violent enough to blow their wings forward over their heads

There is, however, evidence of the existence of special aerodynamic sense organs on Acridids, in the shape of patches of hairs on the frons and vertex which are sensitive to the flow of air past the head (Boyd & Ewer 1949, Weis-Fogh 1949) Stimulation of these has been shown to initiate flight itself once the insect is deprived of a foothold and, during flight, to initiate contra-lateral (compensatory) turning responses when the air flow comes from one side instead of dead ahead These responses could clearly have a stabilizing effect on the locust's flight direction, correcting its own deviations from a straight course, like the halteres of flies (Pringle 1948) Since the same receptors would presumably record a change in the wind direction, if that were sufficiently sudden, the responses could, conceivably, serve to orient the flying locust on the wind, but this is more conjectural

At present, there is no observational evidence that locusts do orient themselves to the wind by such direct responses The fact that the observed responses to wind changes were less marked away from the ground, where the wind is stronger, than they were close to it (p 209), argues against direct responses to air movement participating in course and track determination, however important they may be in securing stability in flight Moreover, if it is only the large-scale air eddies which are so shaped as to give the locusts pushes which are biased in the wind direction, while between these the insects are subjected to more numerous, randomly directed pushes, then it becomes very difficult to conceive how the insect could utilize its aerodynamic sense organs for orientation to the wind It is also difficult to see, at present, how the same organs could be used, without confusion, for regulating two quite different kinds of changes in the insect's relations to the air · both the changes due to its *own* aberrations, of pitching, rolling and yawing (that is, for flight stabilization), and, at the same time, the changes due to aberrations in the *air's* movement, independent of what the insect is doing, such as gusts (that is, for wind orientation, etc) On the other hand, it would seem an economical employment of the means at its disposal if the insect used its aerodynamic sense organs, which are essentially directional *accelerometers*, for flight stabilization, and used other sense organs, such as the eyes, which can act as directional *speedometers*, for wind responses

It remains to consider the effects of the wind as a direct stimulus acting on *settled* locusts When the locust is resting on the ground it has a fixed standard of reference and is therefore in a position to sense and respond to the direct mechanical pressure of the air even when the wind is quite smooth This may well account for the fact that locusts taking off in any appreciable wind are nearly always observed to be oriented into it

It was observed that a sudden lull after a period of strong wind led to mass taking-off by settled locusts (pp 178–181) Since locusts have a powerful tendency to fly spontaneously, the mass taking-off observed as soon as the suppressing influence of strong wind is removed doubtless represents the release of their spontaneous flight activity A drop in wind was followed by mass taking-off over a considerable range of wind speeds, so that the decrease in wind itself rather than a decrease to a certain threshold wind speed was apparently what led to taking-off It seems likely, therefore, that the 'damming-up' of spontaneous flying by wind leads to a situation in which a slight lull, to a wind speed which would previously have been quite effective in suppressing flight, releases flying with unusual unanimity This may be the real significance of Zimin's (1934) observation that gusty winds were particularly effective in causing settled *Calliptamus* to take off Similar observations have been made by Davies (1936) on aphids and Kennedy (1940) on mosquitoes

It is noteworthy, however, that among a number of locusts caused to settle by a gust, those remaining in more exposed, insecure situations took off again sooner than those secure in better shelter (p 181) Locusts settled in a strong wind are visibly affected by it They can be seen bracing themselves against the buffeting, their antennae raised and quivering in the wind Their immediate response is not to fly but to cling tenaciously to their foothold But perhaps this stimulation adds to the strength of the pent-up tendency of the insects to fly, leading to mass taking-off whenever the wind's immediately inhibiting influence is relaxed in a lull Further data are required to decide whether taking-off would occur in this way, as a relief from excessive buffeting

The optomotor theory of behaviour in wind While there is no evidence that flying locusts do, in fact, respond directly to the wind, there is good evidence that other insects make visual compensatory responses to the apparent movement of the fixed background, a movement due to their being carried over that background by the wind The use of fixed visible features for wind orientation has been suggested for many insects, and demonstrated in the laboratory for mosquitoes (Kennedy 1940) It would, on the whole, be more surprising if locusts did not respond indirectly to wind in a similar way than if they did What positive evidence is there that they do so react?

Perhaps the best evidence comes from observations of flight over water (pp 192–193) When locusts were flying low against the wind over tree-dotted farmland, and the wind increased to more than their air speed, they either reoriented down-wind, or flew lower, or even settled; they never underwent a sustained backward drift But locusts flying over water did not appear to react to the wind in any of these ways and were, therefore, drifted backwards The locusts over water did not react to the wind either directly or indirectly, while those over the land did Beall (1941, 1942) made somewhat similar observations on Monarch butterflies (*Danaus plexippus* L) Such behaviour is consistent with the idea that active responses to the wind require a visible background, the features of which, when prominent as on coarse-patterned land, may induce responses up to a fair height, but when small and inconspicuous, as on reasonably calm water, induce responses only at a much lower level

Comparable, but less clear-cut indications that reactions to wind were in fact reactions to the apparent movement of the background pattern, came from the observations over land Locusts flying well above the ground appeared to be less consistently oriented into wind and less responsive to changes in wind speed than those seen flying close to the ground at the same time (pp 177, 179 and 183–185) This is the opposite of what we should expect if the wind acted mainly as a mechanical stimulus, for its speed increases with height But it is just what we should expect if the wind acted mainly indirectly, through visual responses Both the apparent size of the elements in the background pattern, and their apparent speed of movement, decrease with increasing height above the ground, so that the movement of a given background pattern would often be inappreciable to higher fliers while remaining noticeable enough to evoke responses from lower fliers

The field observations thus suggest that the behaviour of locusts in wind depends on optical responses to the apparent movement of the ground, such as have been demonstrated in the laboratory for mosquitoes (Kennedy 1940) But the field data on locusts are made up to a great extent of impressions, hardly adequate material, by itself, for proving the optomotor basis of locust behaviour in wind Let us, therefore, first recapitulate the experimental results with mosquitoes and the theory deduced from them, and then see if the locust data are consistent with this theory

The mosquitoes, *Aedes aegypti* L , were tested in a small wind tunnel over a striped floor They showed a strong preference for flying against the wind They maintained a ground speed of about 17 cm /sec , both in still air and also against winds up to 33 cm /sec , so that in the latter case their air speed was about 50 cm /sec When the wind speed reached 100 cm /sec , their air speed could usually be increased no further and the mosquitoes were flying without making any headway But, rather than turn or allow themselves to be carried backwards, they then alighted on the floor With the air and the floor stripes still, the mosquitoes flew in all directions If the floor stripes were then moved, the air remaining still, mosquitoes flying against the direction of stripe movement reduced their air speed, wavered and then turned right round to fly with the stripes By the time the stripe speed reached 13 to 17 cm /sec all the mosquitoes were flying in the same direction as the stripes They often flew faster but never more slowly than the stripes, increasing their air speed as the stripe speed increased

Now the wind, carrying an insect, creates for it an apparent movement of the background which is in the direction opposite to the wind's own direction, so that a preference for flying against the wind is the visual equivalent of a preference for flight with moving stripes Thus the mosquitoes' behaviour in moving air over still stripes, and over moving stripes in still air, evidently both depend on visual responses to the movement of the stripes relative to the mosquito, and experiments in darkness provided direct proof of this The movement of a stripe relative to the mosquito can stimulate it only as an image passing over the retina, and a given retinal velocity can be produced by the mosquito's flight alone, by its being carried by the wind as well and, in experiments, by movement of the striped floor.

These facts indicate that the mosquito has a *preferred retinal velocity*, divergences from which evoke compensatory responses Three types of response were observed

(1) change of air speed,
(2) change of orientation,
(3) settling

In the original account of this work it was suggested that compensatory responses were evoked whenever the retinal velocity departed from some supposedly 'normal' range that experienced in free flight in still air over a still background This suggestion took no account of the fact that the retinal velocity experienced under such conditions would vary with the insect's height above the fixed background, for this point was not examined in the experiments in the small wind tunnel The more familiar concept of a *preferred* retinal velocity is introduced here in place of the indeterminate 'normal' velocity By the preferred velocity is meant simply that which the insect's various responses tend to restore, and it is apparent that *what is preferred is the movement of images directly from front to back over the eye, at a certain moderate rate*

Thus the various responses are not compensatory in the absolute sense of serving to nullify all movement of images in the eye, that would render locomotion impossible in the presence of visible fixed objects Nor are the three types of response independent of one another They are all evoked only by deviations from a tolerated or preferred retinal velocity and form an integrated system, one kind of response being replaced by another when the first fails to restore the preferred retinal velocity For example, when the speed of movement of images from front to back over the eye is reduced by a head-wind, the insect compensates by increasing its forward air speed When the speed of image movement from front to back is reduced to *nil* and movement begins in the opposite direction, owing to a head-wind so strong that the insect cannot compensate by further increasing its air speed, the insect counteracts the tendency to backward drift in another way, by settling When the speed of image movement from front to back is increased, by the movement of floor stripes against the direction of the insect's flight, it compensates by reducing its air speed When this fails to restore the preferred retinal velocity because the stripe speed is too high, the insect compensates in another way, by turning round and flying in the same direction as the stripes, thereby reducing the front-to-back retinal velocity When the same situation of excessively fast front-to-back image movement is created by a tail-wind, the insect turns round, into wind, with the same result

Similarly, it was suggested that when the images pass transversely, say from the left to right instead of directly from front to back over the eye, owing to a cross-wind from the right, the insect compensates by following the direction of the transverse image movement, that is, by turning toward the right until it is facing into the wind and transverse image movement has therefore ceased That kind of compensatory response was held responsible for the insects' strong preference for flying against the wind rather than in any other direction It is now suggested, further, that this kind of reaction, determined mainly by the *direction* of image movement over the eyes, may be what prevents the insect from abandoning its up-wind orientation even when the *speed* of the image movement has fallen well below the preferred value and could be raised by turning down-wind

Although less precise, the field observations on locusts are at least consistent with the experimental observations on mosquitoes The locust evidence is weakest concerning the regulation of air speed according to wind speed (pp 201–202) This type of reaction was recorded only as an impression, and only in observations on low flights against the wind Reduction of air speed when flying down-wind, which would be equivalent to the mosquitoes' reduction of air speed when flying against moving stripes, could not be detected among locusts in the field, if only because they passed too quickly from view Reduction of air speed by mosquitoes flying down-wind in the wind tunnel could not be detected either, for a similar reason, the insects were quickly deposited on the end wall of the tunnel

The locust evidence is better in the matter of orientation (pp 182–193), with an apparent preference for up-wind courses, and a definite refusal to be carried backwards, when flying near the ground This preference seemed to become more marked as the wind speed increased up to the point where settling began, as among the mosquitoes

The third type of response noted among the experimental mosquitoes, settling when forward ground speed is drastically reduced by a strong head-wind, was clearly evident among low-flying locusts The field observations emphasized an aspect of this behaviour which was detectable but not remarked upon in the small wind tunnel, viz that settling is merely the end-point of a change-of-altitude response to excessive wind (pp 178–182)

So far, therefore, the field observations on locusts parallel the experimental observations on mosquitoes sufficiently closely to warrant a strong presumption that locust behaviour in wind is also governed by optomotor reactions The optomotor theory thus proposed for both mosquito and locust behaviour may be summarized as follows *any image movement over the ventral ommatidia which diverges from the preferred velocity (rate and direction) evokes compensatory responses*

There were some new features in the field behaviour of the locusts, such as changes of behaviour with height and the emergence of a preference for down-wind courses among higher fliers in strong winds Such effects could not have been expected in the wind-tunnel experiments, for the mosquitoes were there forced to remain close to the 'ground' and had little room to manoeuvre in the horizontal plane also But here again it seems unwise to use the largely impressionistic locust observations directly for an extension of the optomotor theory to free-air conditions Instead, it is proposed to start from the firmer basis of the mosquito findings, with which the locust observations do not conflict, and work out hypothetically what would be the consequences of the optomotor theory under free-air conditions Given the pattern of behaviour to be expected with various combinations of wind speed and height of flight, we can then re-examine the locust observations and see how far they conform to it

The optomotor hypothesis of field behaviour in relation to wind speed and height In elaborating this hypothesis we postulate not only the three types of compensatory response and the preferred retinal velocity, but also a *preferred air speed*, departures from which provoke compensatory responses of the same three kinds There is good evidence that gregarious locusts are very persistent fliers, which immediately sets a lower limit of preferred flight exertion, at somewhere above zero air speed The long continuance of locust flying makes it seem likely, on general grounds, that there is also an upper limit beyond which they exert themselves only under pressure, preferring a moderate, 'cruising' air speed At present there is no quantitative evidence of such a preferred air speed, however, and in any case it presumably alters with the condition of the locust But if there were only a preferred retinal velocity and no preferred air speed, then one might expect swarms would quickly shear apart from the top down, the higher fliers racing ahead (during up-wind flight) to compensate for the lower retinal velocity due to their greater height, since retinal velocity decreases with height faster than the wind speed increases with height

For simplicity of exposition, only courses directly up- or down-wind will be considered here The detailed process of turning from one course to another and the not uncommonly observed maintenance of cross-wind courses are not considered, because the available data are inadequate and the hypothetical analysis would require further and more complicating assumptions

The height-wind speed hypothesis is best explained by means of diagrams These must be very schematic and are constructed for the present without any numerical scales or assumed values for the preferred retinal velocity and air speed The co-ordinates in all the diagrams are height above the ground and wind speed, the latter being assumed for the present not to vary with height The logical consequences of the various assumptions made are shown, by cumulative stages, in figure 13

The most obvious consequence of the optomotor theory is that locusts flying sufficiently high will not show any compensatory responses to the wind, simply because they receive no optomotor stimulation We may then describe them as above the *maximum compensatory height*

The postulated 'preference' for a particular retinal velocity did not refer of course to a subjective preference for some ideal situation The term preference is merely a convenient way of expressing the net result of the insects' reactions to changes in their retinal velocity The postulated preference assumes *some* movement of images of background objects, with immediate changes in that movement whenever the wind speed or direction changes, or when the insect changes its air speed, direction or height In the complete absence of such image movement, and when therefore nothing the wind or the insect does produces any immediate change in its retina, we assume it does not 'react' that is, no behaviour changes result from this situation in itself

The maximum compensatory height can be set in two ways With a given 'grain' size in the background pattern, there will be a definite height, independent of the wind speed, above which the locusts' eyes fail to resolve the separate elements in the pattern (figure 13*A*, *JJ*) Below that height they will be able to resolve the pattern and so be able to be stimulated by its apparent movement, provided that movement be at an appropriate rate

Even if the background pattern can be resolved up to infinite height, the movement of images of the insect's eye will sometimes be too slow to evoke any responses It will be fast enough to evoke them only if the insect's ground speed is above a certain value, which will increase with its height It is a familiar experience that when one is travelling, near objects appear to move faster than distant ones During flight, the retinal velocity of images of the ground must be proportional to height Hence the height at which the image movement

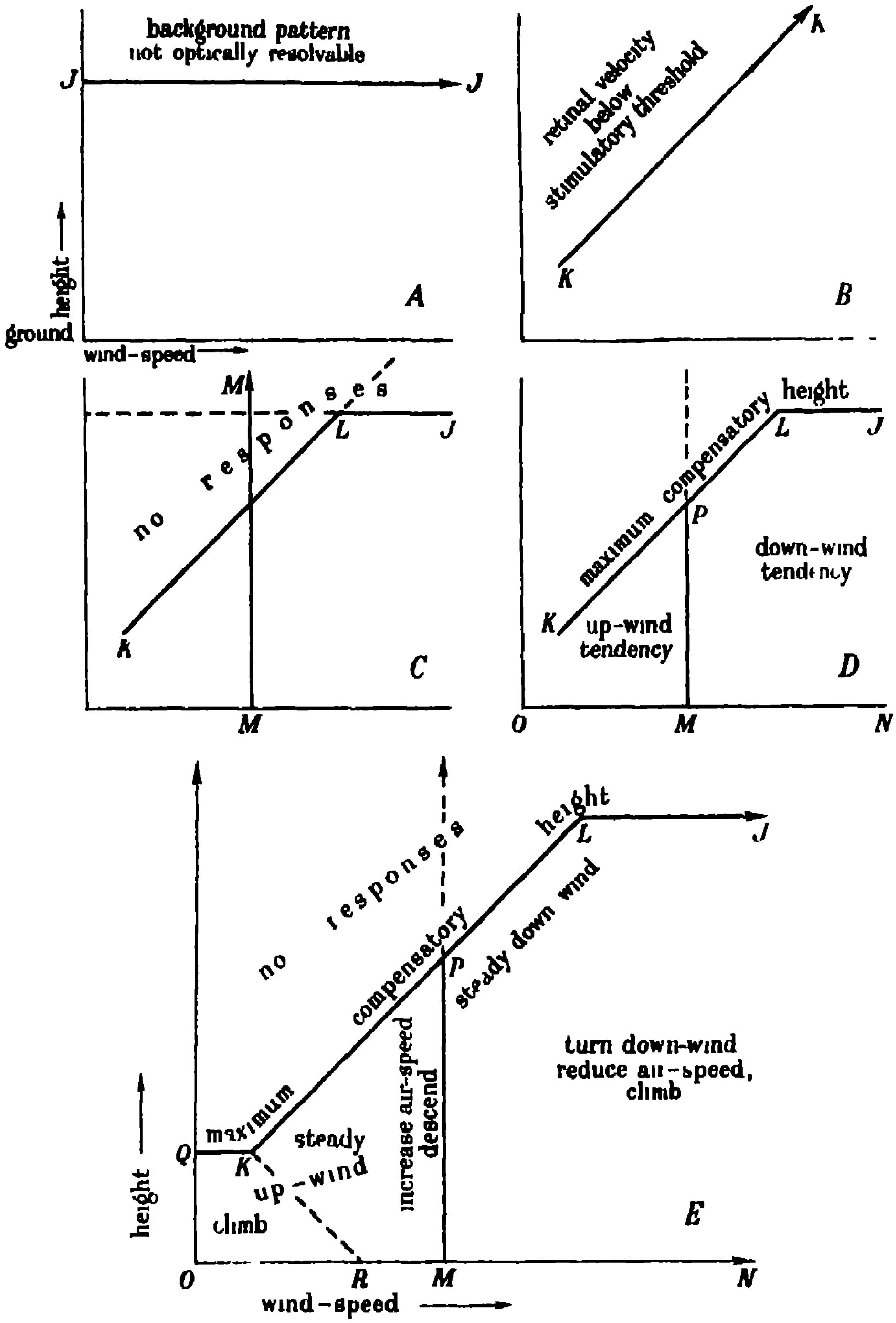

Figure 13 Diagrams illustrating the optomotor hypothesis of the behaviour of flying migrants in relation to wind speed and height above the ground Explanation in text, pp 212–215

over the eyes of a rising locust will become too slow to evoke compensatory responses will depend on the speed of the wind carrying the locust, as well as on its own air speed and course, for its ground speed depends on all three The stronger the wind, the higher the locust can rise before its apparent ground speed (retinal velocity) will fall below the stimulatory threshold (figure 13*B*, *KK*)

These two kinds of limitation, illustrated in figures 13*A* and *B*, are combined in figure 13*C*. With the field observations in mind it is assumed that, over the range of wind speeds with which we are dealing, the limiting factor is usually the locust's inadequate ground speed Only when the wind speed is very high, along *LJ* in figure 13*C*, do we assume that non-resolution of the background pattern sets the height limit for optomotor responses Thus the first consequence of the optomotor theory is that there will be a *maximum compensatory height* along *KLJ* in figure 13*C*, which increases with the wind speed as long as the locust's eyes are capable of resolving the background pattern Correspondingly, there will be a *minimum compensatory wind speed*, also along *KLJ*, which increases with height

Above the maximum compensatory height the locusts' movements will be affected only mechanically by the wind Their courses will not be affected by the immediate wind, unless they can orient by reactions to mechanical pressure changes (see pp 206–208) The courses of the insects will not necessarily, of course, become random in this situation They will not depend on the immediate wind, but will depend on reactions to other environmental features which can still provide effective stimuli, such as fellow locusts or the sun But the *tracks* of the insects will be biased more and more down-wind as the wind speed increases If we enter a vertical line *MM* in figure 13*C*, where the wind speed is equal to the locusts' maximum air speed, then to the right of this line all tracks must be more or less down-wind

A complication that arises in fixing the position of the maximum compensatory height is that the locusts' own air speed is a finite quantity which is added to the wind speed during down-wind flight and subtracted during up-wind flight With a given locust air speed and wind speed, the ground speed will therefore be higher for down-wind than for up-wind fliers, so that the maximum compensatory height will also be higher for the down-wind fliers, other things being equal On the other hand, for compensatory responses to be evoked, the front-to-back image movement which down-wind fliers experience must be considerably faster than the back-to-front image movement which up-wind fliers experience when they lose headway in strong winds On this count, the maximum compensatory height will be higher for up-wind than for down-wind fliers As a first approximation we shall assume these two opposite biases balance, and not complicate the diagrams by postulating different maximum compensatory heights for up-wind and down-wind fliers

Now let us turn to the region below the line *KLJ*, in which the locusts are subjected to effective optomotor stimulation Here the critical wind speed, which equals the locusts' maximum air speed, separates two regions in which not only the tracks, but also the effective responses of the locusts must differ In the region to the right of *M*, bounded by *NMPLJ*, the locusts cannot progress directly into wind and will therefore turn more or less down-wind, so long, of course, as they remain air-borne In the region to the left of *M*, bounded by *KPMO*, the locusts can progress directly into wind and will, if there is enough wind, set course against it, according to the theory (pp 210–211), again, of course, so long as they remain air-borne Flying on up-wind courses to the left of *M*, and down-wind to the right of *M*, are therefore entered as the characteristic *tendencies* in figure 13*D*

The situation will be further differentiated within each region (figure 13*E*) In the upper part of *NMPLJ*, near the line *PL*, turning down-wind will be a completely successful compensatory response The locusts there will be high enough not to experience too great a retinal velocity even when the wind speed is added to their own air speed They will be able to fly both at their preferred air speed and with their preferred retinal velocity, so that under these height-wind conditions down-wind flight can become established as a level, steady course Lower down, the retinal velocity will be too high in down-wind flight, leading to a reduction of air speed and, since this departure from the preferred air speed will evoke further compensation, to climbing until the retinal velocity falls to the preferred value at the preferred air speed No stable combination of height, air speed and course seems possible in this region

In the right-hand part of *KPMO*, near the line *PM*, up-wind flight will be very persistent, but cannot be entirely stable because it involves raising the air speed above the preferred value, and even so the retinal velocity will often be below that preferred, especially for fliers up near the line *KP* Descent will raise the retinal velocity, but periodic rests may be the only adequate compensation for the high air speed necessary in these conditions In lower wind speeds, somewhat below the insect's preferred air speed, up-wind flight can become established as a level, steady course But as we pass into the region of very weak wind close to the ground, the wind's contribution to the insect's retinal velocity becomes eventually insignificant, relative to the part played by the insect's own air speed and course The locusts' behaviour will no longer be appreciably affected by the wind

At the same time, since the insects are very near the ground in this region *QKRO*, merely flying at their preferred air speed will itself create a retinal velocity in excess of that preferred Reduction of air speed would lead to further compensation, but a successful response will be to climb The height to which the insect must climb will decrease with the wind speed as indicated by the line *KR* When the wind speed is negligibly small, near *QO*, the maximum compensatory height will now depend solely on the insect's air speed It will be virtually independent of wind speed, hence the line *QK* is drawn horizontally

The optomotor theory is not new in principle and assumes a fairly simple set of interdependent reactions But it is abundantly clear that this theory, so far from leading one to expect some simple, fixed relation between wind direction and locust flight direction, provides the basis for a pattern of behaviour in the field which is decidedly complex and fluid, even when treated schematically as above Before considering the actual field observations some further complications likely to occur in the field must be mentioned

Even over a level plain, wind speed is not uniform As one approaches the ground, the influence of friction becomes increasingly great, so that the wind speed becomes progressively lower That is to say, in following the hypothetical behaviour of a locust rising from the ground, it would be wrong to read vertically up the diagram (figure 13*E*) The conditions experienced by a locust in climbing flight would be represented by a series of points on a line inclined upwards and to the right Consequently it would be theoretically possible to see individual locusts behaving in the following way at one moment, but at different heights fairly near the ground, in stable up-wind orientation, higher, oriented up-wind at increased air speed, higher, in the region where no stable orientation is to be expected, higher still, in stable orientation down-wind, and higher still, totally unresponave to the wind Such a confused picture would nevertheless be entirely consistent with the optomotor hypothesis

Moreover, the wind is at all times irregular in structure and often distinctly gusty, whereas the behaviour indicated in each part of figure 13*E* assumes a steady state Hence instantaneous field records of locust courses occurring in conjunction with particular wind speeds and directions cannot be expected to conform fully to the hypothesis, because the immediately previous wind speed and direction of the locusts recorded will have been different This will apply especially to higher fliers

Finally, it should be noted that quite different types of compensatory responses may intervene when optomotor responses to wind are weak or not evoked at all For example, it is conceivable that a locust, having had an up-wind orientation imposed on it while near the ground and having at the same time established a light-compass orientation to the sun, will retain this after climbing to greater heights, where optomotor responses to the ground would not occur Again, if a deep swarm is flying up-wind, the locusts near the ground being subject to strong optomotor responses to ground movement and taking up the consequent orientation, the whole swarm might retain a stable up-wind orientation through gregarious alinement This seems especially likely if there is vertical circulation in the swarm, as there often is These other types of compensatory response would therefore be capable of perpetuating orientations imposed by the wind after the insects had ceased to respond to the wind itself, for example, when the wind dropped below the minimum compensatory speed for the given height, or the locusts rose to above the maximum compensatory height for the given wind Finally, and perhaps most important, responses to stimuli quite unconnected with the wind may dominate the insects' behaviour, even in circumstances when clear wind responses are expected theoretically All such effects would make analysis of the wind's own optomotor effects doubly difficult in the field

How far, nevertheless, do the field observations conform with the optomotor hypothesis of behaviour in relation to wind speed and height? The records refer to locusts flying fairly near the ground, of necessity, so that the eventual complete disappearance of wind responses at some height above the ground, assumed by the hypothesis, remains unconfirmed The existence of a maximum compensatory height due to failure to resolve the elements in the background pattern is, however, suggested by the failure of responses among locusts *over water*, by contrast with their behaviour at the same height and in the same wind over nearby land (pp 192–193 and 208) In the field, where, of course, the wind speed varies all the time, one would not expect to see a constant failure of responses above any particular level, but would expect rather to find a tendency for responsiveness to decrease with height Thus, the existence of a maximum compensatory height, due to the apparent ground speed being too low even when the background pattern is resolvable, is in fact suggested by the observations that stronger winds were required to evoke responses from higher than from lower fliers (pp 177, 179 and 185) The same observations suggest that insufficient retinal velocity, rather than the indistinctness of the background pattern, was what usually set the height limit to optomotor responses over land

The numerical data summarized in figure 11 (p 191) further support the supposition of responsiveness decreasing with height, but increasing with wind speed at a given height. The preponderance of up-wind courses was greater below than above 8 m in winds up to

4 m /sec., and was greater in winds of 1 to <4 m /sec than of less than 1 m /sec In winds of 1 to <4 m /sec the preference was sharper even over 8 m than it was in winds of less than 1 m /sec below 8 m

The smaller proportion of up-wind courses among higher fliers was not merely due to the wind speed increasing from the ground upwards, making it more difficult for insects farther from the ground to make progress against the wind What happened in winds of 4 to 7 m /sec , against which progress definitely was difficult, can be seen in the third lower diagram in figure 11, a preference for down-wind courses (as against across-wind ones) was added to the preference for up-wind courses But in winds of less than 4 m /sec , there was no down-wind preference among higher fliers, which nevertheless showed a weaker up-wind preference than did lower fliers This was evident even when the wind speed near the ground was less than 1 m /sec and the ground was free of obstructions The wind 8 m above such ground could hardly reach 4 m /sec when it was less than 1 m /sec near the ground

The fact that the data for winds of 4 to 7 m /sec in figure 11 show a more clearly defined orientation preference among higher fliers than among lower ones does not mean that the lower fliers were less responsive When watched continuously the lower fliers always seemed to be more responsive, but in these strong and gusty winds their responses were variable and did not result in steady flying in any one direction

If responsiveness did decrease with height but increased with wind speed, as required by the hypothesis, what of the responses themselves? The collected records in figure 11 and the continuous observations figure 11 fairly reflects, show the up-wind preference in more moderate winds and down-wind preference among higher fliers in stronger wind, which are expected on the hypothesis No down-wind *preference* is shown among the records for lower fliers in stronger winds, but the postulated tendency to turn down-wind was observed, and the general instability of behaviour under these height-wind conditions also accords with the hypothesis The postulated tendency for up-wind fliers to descend and even settle when the wind speed increased to around their air speed was unmistakably observed

A noticeable feature of the observed behaviour which is not expected on the hypothesis was the tendency of fliers caught in winds of 4 or more m /sec to descend also Hypothetically, ascent rather than descent is expected under such conditions, and the observations demand closer examination In most cases when such descents were definitely observed the locusts had been progressing against less strong wind, had then been caught by a gust and had descended before turning round Such descents are in accordance with the hypothesis, for as long as the insect retains its up-wind orientation and makes even a little headway, descent will raise the front-to-back retinal velocity toward that preferred, even if the wind speed is the same at the lower level Often the wind speed will be less nearer the ground, and descent will then enable the insect to prevent image movement from back to front and increase its rate from front to back, with less effort Ascent would have the opposite effects, still further reducing the rate of front-to-back image movement and increasing the likelihood of actual back-to-front movement The conflict between observation and hypothesis here is more apparent than real, *fluctuating* wind conditions having been left out of account in the hypothesis as presented Strictly speaking, locusts descending while holding their ground facing up-wind, and are in conditions to the left, not to the right of *M* in figure 13*E* (p 213)

The situation becomes rather different if the locust has already reoriented down-wind as a compensatory response Such fliers, it is true, often turned up-wind again before descending and always did so before actually settling But what of descents made while still oriented down-wind? When the locust is high the rate of front-to-back image movement may be less than that preferred, and descent to an intermediate level will increase the rate to the preferred value But low-flying locusts, having been turned down-wind by a gust, will at once experience excessively fast front-to-back image movement and descent will make it even faster Ascent would be expected on the optomotor theory, yet such ascents were rarely observed Possibly that was because locusts were rarely seen in winds which were strong enough, and remained so for long enough near the ground, to prevent the down-wind fliers there from turning up-wind again and *then* descending, before an ascent while still oriented down-wind became the only successful form of compensation left to them

It should be emphasized that while low, down-wind flying locusts were never seen to ascend, except in a gale, it is not as certain that they definitely descended, as it is that up-wind fliers and higher down-wind fliers definitely descended, in strong wind Low, down-wind fliers passed the observer quickly, and it was not easy to follow the individual by eye and distinguish its descent from that of neighbouring up-wind fliers The latter's descents were more certainly observed as they remained near the observer for longer

The remaining part of the hypothesis, postulating a tendency to climb away from the ground when the wind speed falls well below the locusts' air speed, is consistent with the frequent observation that locusts not only descended in gusts but also rose actively into the air in lulls (pp 178–181) If it seems at first strange that an active flier might need some inducement, such as an excessive retinal velocity, to make it rise away from the ground, that is only because it seems eminently 'logical' that it should rise, but this is not, of course, in any immediate sense a causal explanation of the behaviour

Figure 12 (p 192), which illustrates the orientation observations on semi-migrant locusts, shows, like figure 11 for full migrants, a predominance of up-wind courses among low-fliers with weak winds, but courses become random in direction at lower wind speeds than with migrants, which is to be expected from the lower air speed of semi-migrants The more random courses of higher fliers at low wind speeds is again in accordance with expectation

The field observations, so far as they go, are thus generally consistent with the elaborated hypothesis of optomotor behaviour and hence provide considerable support, short of direct proof, of the more general optomotor theory of reactions to wind

We cannot at present assign any reliable values to the postulated preferred retinal velocity and preferred air speed of these locusts, but even very rough estimates might have some working value until superseded If these two speeds are indeed preferred, one might be able to gain a rough idea of them from one's impression of 'average' behaviour The preferred air speed might be put at about 3 m /sec , and the preferred retinal velocity at that experienced by a locust flying up-wind at about 6 m above the ground with a ground speed of 3 m /sec If so the preferred velocity will be experienced also at 2 m high with a ground speed of 1 m /sec , 10 m at 5 m /sec , and so on In figure 13E (p 191), M might fall at about 6 m /sec , R at 3 m /sec and Q at, say, 6 m

It is worth dwelling upon the new feature brought out by the locust observations which was not observed in the mosquito experiments and therefore not then considered in terms of compensatory reactions: the tendency to turn down-wind in strong winds.

The wind tunnel used in the mosquito experiments was so small that the insects reached the floor and alighted almost at once when unable to make headway against the wind The sequence of events had they not been able to do so was not investigated In the open air, when locusts were carried back by the wind and did not immediately settle, they turned away from their up-wind orientation Sometimes they took up an across-wind course in which they were still able to make at least some headway over the ground, but if they stayed in the air they tended to turn right round and face due down-wind, even when some headway was being made in the across-wind orientation (pp 184–193) Locusts in a gale, which seemed to stimulate continued flight with no possibility of making headway against the wind were oriented consistently down-wind (p 183)

There are two questions here first, why the locusts turn down-wind at all, and second, why down-wind courses predominated among higher fliers but not among lower fliers An insect wavering to one side, with the onset of back-to-front image movement, would be able to reach an orientation where there was no longer any actual back-to-front image movement by perhaps quite a small turn And, if hit by a gust in this position, it could eliminate the resultant back-to-front component in its image movement by quite a small increase of air speed, demanding less effort than the larger increase required while oriented directly into wind But having made this turn, it would of course be drifting sideways and experiencing transverse image movement in a roughly up-wind direction This should, on the theory advanced for up-wind orientation, evoke a compensatory turn up-wind Given a wind speed higher than the insect's maximum air speed, however, such an up-wind turn could not be a successful compensatory response, for it would demand an increase of air speed which the insect cannot make Yet what the insect actually does, turn down-wind, will not be a completely successful response either, for the front-to-back image movement it experiences while flying down-wind will be excessively fast In fact, as was apparent in the field, such locusts are in an unstable condition

It seems that, for a locust faced with this dilemma, direct front-to-back image movement at an excessive rate is more tolerable than transverse image movement at a somewhat less but still excessive rate, as well as more tolerable than even quite slow back-to-front movements, so that the down-wind orientation is taken up

Two possibilities should be kept in mind with regard to this down-wind orientation First, there must be an upper as well as a lower limit of retinal velocity at which optomotor responses fail It may be that the image movement, being at its maximum rate in down-wind orientation, becomes so fast in a strong wind as to be blurred, a situation equivalent to no image movement and evoking no response The actual turn down-wind might also be aided by the increasing blurring of all images experienced as the insect's translation over the ground becomes faster and faster, once it begins to turn Also, some authors (see Kalmus 1949) have observed walking flies making optomotor responses, not only of the compensatory type in which the insect moves in the same direction as a moving background, but also responses in the opposite sense, in which the insect walks *against* the direction of the moving background It is not clear what conditions are necessary for such responses to appear Turning and moving with the wind is the visual equivalent for a flying insect of turning and moving against a moving background in still air In both cases the insect moves against the direction of apparent background movement It would be worth investigating whether, when the insect can no longer make headway against the wind, that is, when it is in a situation where ordinary compensatory responses cannot be 'successful', this causes a switch-over from the first, compensatory type of optomotor reaction to the second, opposite type of optomotor reaction

For higher fliers, the stability of down-wind courses was expected from the hypothetical analysis, because a locust can achieve its preferred retinal velocity and air speed while oriented down-wind in a strong wind while it be fairly high, but not if it be low But to some extent the greater duration of down-wind courses among high-fliers could be attributed to the mere fact that they took longer to complete the other type of response to strong wind, descent (p 192) The tendency to turn down-wind in excessive wind has less chance to show itself among low-fliers, for among them it is cut short by settling or by entry into a slower-moving air layer near the ground

The optomotor theory in the literature The optomotor theory of wind orientation has been discussed by Fraenkel (1932), de Lépiney (1928, 1933), Williams (1930, 1942, 1949), Gunn *et al* (1948) and Waloff & Rainey (1951) None of these authors has, however, quoted observations with the accompanying information on both wind speed and height of flight which would help to decide for or against the optomotor theory Fraenkel recognized that the necessary evidence was not yet available He called, in particular, for information on wind orientation over a uniform substrate such as the sea (Fraenkel 1932, p 205) Just this kind of evidence in favour of the optomotor theory of wind orientation is now available for locusts (pp 192–193), but at that time Fraenkel could refer only to the fact that insects were nearly always reported as having crossed the sea with particular winds, and this kind of circumstantial evidence is also now available in detailed form for locusts (Waloff 1946*b*, Rainey & Waloff 1948) Fraenkel emphasized the difficulties facing any alternative theory which assumed a direct orienting action by the wind, and the absence of any need to create such a theory in view of the experimental evidence that an optical mechanism was concerned in the analogous case of orientation against a stream of water (rheotaxis)

De Lepiney (1928, 1933) mentions the hypothesis of wind orientation by optical compensatory responses to the apparent movement of the ground, but dismisses it along with several others He does so on three grounds that the course of the various swarms he saw remained very much the same for hours and days together while their tracks varied greatly according to the wind, that the eyes of locusts are not directed downwards, and that on close approach to the ground, and only then, do locusts appear to react to objects there With regard to the last point, distinct reactions to particular objects are not under consideration here, but rather reactions to the apparent movement of the whole array of objects forming the visible substrate With regard to the second point, de Lépiney's statement that the eyes are not directed downwards does not seem to be based on any published work Vertical transverse sections, for example, have not been published for *Schistocerca* The 'pseudo-pupil' of *Schistocerca* (Roonwal 1947) can be followed down in the transverse plane to within about 30° of the vertical, but the anatomical meaning of this phenomenon has yet to be determined with certainty

De Lépiney's first objection does not seem justified by the observations he quotes He mentions 50 m as the maximum height at which he observed swarms flying, but does not say what was the normal height If, for example, the swarms observed by him were flying mainly over 10 m above the ground and the winds were generally weak, then one would not expect optomotor responses to wind to occur One would expect what he describes tracks varying according to wind direction and strength, but course remaining relatively constant (figure 8*A* and *B*, p 187), through the joint action of the light-compass reaction to the sun and gregarious inertia (p 243) It is probable the winds were rather weak at the time of de Lépiney's observations, for they were made at a period (winter) when the whole migration trend is against the prevailing wind in North Africa

Williams (1942) questioned whether the laboratory demonstration of wind orientation by visual means (Kennedy 1940) would have any bearing on behaviour in the field, for the experimental mosquitoes were at most only 10 cm above the visible background, and the apparent movement would be much slower at normal flying heights outdoors

The diminished rate of apparent movement resulting from merely increasing height is fully recognized in the hypothesis now put forward Given an adequately patchy appearance of the ground, a given retinal velocity can be produced at any height, but the ground speed required will be proportional to the height It is for this very reason that a locust becomes less restrained in its orientation and speed as its height increases (figure 13*B*, p 213), without any change whatever in its compensatory behaviour It may very well be that the ground is sometimes not adequately patchy (figure 13*A*), that appeared to be so as low as 5 m in the case of the wavelets on a lake, but considerably higher over land (pp 192–193) Although the figures given on p 218 are very rough estimates, they do suggest there is no intrinsic difficulty in envisaging the wind as an important orienting influence acting via optical responses to apparent ground movement, in the field as well as in the laboratory

Rather better estimates can be made for mosquitoes It was found that mosquitoes began to show a noticeable preference in orientation, by ceasing altogether to fly against the direction of moving floor stripes, when the stripe movement exceeded about 0 15 m /sec At considerably lower stripe speeds flight in this direction was already slow, wavering and less frequent than flight in the opposite direction If we take 0 10 m /sec as a generous estimate of the minimum stimulatory stripe speed for a mosquito flying against the stripes and 10 cm above them, and if we take 0 15 m /sec as the mosquito's air speed, then the minimum stimulatory ground speed will be 0 25 m /sec If so, the minimum stimulatory ground speed will be 2 5 m /sec at 1 m above the stripes, 25 m /sec at 10 m , and so on Hence the maximum height at which the mosquito will receive effective optomotor stimulation, in a 1 m /sec wind, will be $(1+0\ 15)/2\ 5 = 0\ 46$ m , in a 10 m /sec wind it will be 4 6 m , and so on These estimates of the maximum compensatory height for mosquitoes seem in fact too low, for the writer has observed various midges, mosquitoes and may-flies swarming up to 2 m away from the nearest fixed object and maintaining their position against the gentlest breezes, by closely regulating their air speed and orientation

In place of the optomotor theory of behaviour in wind, Williams (1930), concerned primarily with butterfly migration, advanced the suggestion that migrants are guided by an innate sense of direction regardless of the wind Without details as to wind speed and height of flight the data on butterfly directions cannot be compared with the locust data, but Williams has applied his suggestion to other features of behaviour in wind for which comparable locust observations are available He quotes two butterfly observers as recording an inverse relation between wind strength and height of flight, the insects coming low when the wind was strong, but rising in little or no wind The present author has observed the same behaviour, not only in locusts (pp 178–182) but in many insects, including butterflies. Williams concluded from the observations he quoted, together with others in which high-flying butterflies were seen oriented with the wind but low-flying ones against it, that 'butterflies may take advantage of a following wind by rising higher, and avoid a contrary wind by keeping close to the ground, but that, independent of any wind direction which may occur at the time, there is a direction in which they are urged to go, and they make every effort to keep to it' Here Williams seems to be doing what he describes in another place in the same book as 'appealing to internal unknown or little known forces—thereby leaving the question quite unsettled' To speak of insects 'taking advantage' of a given wind direction is to assume that the insects anticipate which winds will be to their advantage and which will not The optomotor theory demands considerably less of the insects, and will account, as set out above, both for the changes of height with changes of wind speed and for the changes of wind orientation with change of height

Gunn *et al* (1948, p 46) have brought forward a particular form of the optomotor theory of wind orientation which is embodied in their expression 'the forbidden course' Observing that locusts did not maintain steady flight while being carried backwards by the wind, however small the backward component in their ground speed might be, but did fly on a track nearly at right angles to their course, the authors suggested that a course which would lead to any degree of backward drift was 'forbidden' for, that is to say avoided by, the locusts This theory fits some of the facts and enabled Gunn *et al* to narrow down the possible range of courses along which swarms could have flown in given wind conditions But the optomotor responses of flying locusts involve more than the mere avoidance of backward drift Figure 11 (p 191) illustrates the finding that locusts have a preference for up-wind orientation even when winds are gentle enough for there to be no risk of backward drift while so oriented The same applies to mosquitoes (see pp 209 and 221) Hence the suggestion that up-wind orientation was due to compensation of *transverse* image movement even before there is any back-to-front component in that movement (p 210) Such compensatory reactions will, naturally, only occur provided, as with other kinds of image movement, that the rate is neither too low nor too high for the movement to be distinguished The significance of the 'forbidden course' appears to be that, when a back-to-front component does develop, the insect begins to react in a new way, changing over to a different kind of compensatory response now that the old one has failed to maintain the preferred direction of image movement It may descend and even settle, or it turns, now tolerating transverse image movement, and thereby avoiding not only the 'forbidden' back-to-front image movement, but equally the 'forbidden' (excessive) air speed which continued progress directly into wind would demand (pp 184 and 219)

Waloff & Rainey (1951) consider that the preference for roughly up-wind courses at wind speeds up to 3 m /sec (see p 205), could be accounted for satisfactorily without invoking any optomotor hypothesis They suggest that it is due to the mere continuance after take-off, of the up-wind orientation assumed before take-off, when the locust is in a position to respond to the mechanical pressure of the wind (p 208) The continuance of a mechanically stimulated orientation may well contribute to the frequent occurrence of up-wind courses among low fliers, especially in 'rolling' swarms But it is hardly a sufficient explanation, because fliers are also observed very regularly to have assumed that orientation just prior to alighting, whatever their previous course may have been (p 185)

Waloff & Rainey devoted more attention to possible optomotor effects, when analyzing their 'snapshot' readings in relation to very short-term wind fluctuations They examined two possible ways in which the locusts' courses might be adjusted to such fluctuations so as to maintain either a constant angle between course and wind, or a constant direction of displacement over the ground In the event, the analysis demonstrated neither of these kinds of constancy It seems very doubtful whether a limited number of 'snapshot' readings from a wide range of heights in fluctuating wind, could, by themselves, throw any light on the situation The authors did not indeed exclude the possibility of demonstrating an effect of rapid wind changes on the orientation of fliers, with improved techniques, in any case there are grounds (pp 196 and 242) for expecting such effects to be less marked than the effects of longer-term wind changes

Conclusions It will be as well to recapitulate the tentative conclusions now reached concerning the complex matter of wind and migratory behaviour, with special reference to the optomotor theory and the hypothesis elaborated from it The conclusions will be given under the headings of taking-off and settling, speed of flight, height of flight, and direction of flight, but these aspects of behaviour are in practice integrated, in such a way as to create a strong presumption that migrant locusts have both a preferred retinal velocity and a preferred air speed

Taking-off and settling Strong wind has a suppressive effect on taking-off and on flight near the ground, but less effect on flight well above the ground Fliers near the ground are caused to settle by gusts, while taking-off occurs in lulls, so that gusty winds may produce a resultant down-wind movement These facts are consistent with the optomotor theory

Speed of flight The cruising air speed of *Schistocerca* is in the region of 3 m /sec , but when flying close to the ground against a wind of varying speed the locusts seem to stabilize their ground speed by varying their air speed which may then reach 5 m /sec or more for short periods at least Farther away from the ground, air speed seems less influenced by wind speed, and at sufficient height is presumed to be entirely uninfluenced, unless temporarily in very turbulent air These conclusions are also consistent with the optomotor theory, but there is an urgent need for further measurements of air speeds in known conditions

Height of flight, among low-fliers, depends on the wind speed in much the same way as taking-off and settling, locusts ascend somewhat in lulls and descend in gusts This accords with the optomotor hypothesis of a preferred retinal velocity attainable at a height which decreases with the wind speed Higher fliers are less responsive to wind-speed changes in accordance with the hypothesis of a maximum compensatory height above which no optomotor responses occur, this height increasing with the wind speed The optomotor effect of height is quite unconnected with the fact that wind speed generally increases with height, a fact which in no way alters the hypothesis but which does complicate its detailed investigation and application The optomotor effect is geometrical, varying directly with height, whereas the wind speed does not change so fast with height But since the wind speed does increase somewhat with height, locusts climbing in moderate winds will tend to suffer backward drift, compensated by reducing height, with the result that sustained flight in moderate winds should be predominantly up-wind at low heights This seems to fit the available data reasonably well and to agree with one's general impression, but more and more precise field measurements are required

Direction of flight In moderate winds near the ground locusts orient preferentially into wind This preference becomes less marked higher up in the same wind or in weaker winds low down It has already been mentioned that in moderate winds the vertical wind gradient would tend to encourage low flying up-wind At wind speeds around the maximum speed at which the insects will fly they turn away from their up-wind orientation and tend to fly oriented down-wind, especially if fairly high But in this respect, too, they become eventually less responsive at sufficient height All this accords with the optomotor hypothesis which carries the further implication that orientations will be quite unaffected by the wind direction above the maximum compensatory height But further observations are required to establish these conclusions, to express them in terms of actual wind speeds and heights and to determine the preferred retinal velocity and air speed

If these are the conclusions reached by considering the behaviour of an isolated locust, the situation becomes somewhat different with a dense swarm of locusts extending from the ground upwards, for we have to reckon with the reaction of one locust to another In moderate winds the low-flying locusts should orientate up-wind and, even if the high-flying ones are above the maximum compensatory height, they should tend because of gregarious behaviour to fly with their fellows below and therefore up-wind too This tendency should be reinforced by the vertical circulation which takes place within a swarm and the stabilizing effect of the sun-compass reaction, although with very deep swarms the connexion may very well break down

This tendency to up-wind flight by large swarms is likely to be modified when the upper locusts are above the maximum compensatory height, except when the wind reaches the upper limit of air speed The upper locusts are then expected to swing round and fly down-wind, giving the not unfamiliar picture of a shearing swarm, with the lower layer progressing slowly up-wind and the upper layer scudding down-wind, and with interchange taking place between the layers as gusts come and go

Gregariousness

The evidence of gregariousness Evidence that mutual stimulation among swarm adults provides some of the impetus for migration, and is partly responsible for the parallelism of movement within the swarm, has been quoted earlier (pp 193–195) The general grounds for regarding gregariousness as primarily responsible for the cohesion of swarms have been stated by Gunn *et al* (1948)

> 'When large numbers of individuals come together and remain together for long periods while moving through a complex and highly variable series of natural situations with no discoverable common factor other than the crowd itself, one is left with a strong impression that the animals are bound together by reactions to one another'

It might seem unnecessary to stress the real existence of gregarious behaviour among locusts But it is necessary to stress it, since Chauvin (1947) has questioned the existence of both mutual activation and mutual attraction In his view the cohesion of marching hopper bands could be due entirely to their following parallel paths through independent but identical responses to some (unknown) external directing agency Here it is enough merely to recall the frequent occurrence of gregarious re-alinement (p 194) Temporary dispersals and deviations occur too often for the cohesion of migrating locusts to be accounted for by such externally directed, parallel progression

The cohesion of stationary bands Chauvin would again ascribe entirely to independent but identical responses to external stimuli, especially temperature It is recognized that individual responses to topographical temperature differences help to keep stationary bands and swarms together But gregariousness also contributes, for it has been found that positions close to but *not* occupied by basking hoppers do not differ detectably in any respect, including temperature and draughtiness, from the adjacent positions occupied by bands (Kennedy 1939, p 519, Pielou 1948) Writing of *Nomadacris septemfasciata* hoppers on dense tall grass, Pielou says

'The tendency to form dense clusters, in which hopper is often on top of hopper, when there is plenty of grass around for all, is a striking example of gregarious behaviour '

Events during the launching process of swarms (p 193) provide perhaps the best evidence that mutual stimulation contributes some of the impetus for migration On this point, too, the conclusions on adults are supported by observations on hoppers Pielou (1948) describes how an initial slight disturbance sets up a cumulative chain reaction in small hopper bands of *N septemfasciata*, and may lead to the whole bandlet moving off in one direction He goes on

> 'Within four or five seconds this outburst of activity dies down but, before finally disappearing, may build up again and repeat itself in a striking manner without any further obvious external disturbance'

The writer has observed the same sequence of events in small bands of *Schistocerca* hoppers

Pielou's hopper bandlets were evidently in an unstable condition not normally migrant, but easily 'catalyzed' into intense, *self*-sustained activity by external stimuli He emphasizes that his bands were small and that larger, denser bands of the same species migrate more actively One is strongly tempted to conclude from this work, and from the more quantitative work of Smit (1939) on the critical density for migration by *Locusta pardalina* hoppers, that the same hoppers would migrate more actively in large dense bands than in smaller, less dense bands Clark (1950) has actually recorded such differences in *Chortoicetes terminifera* bands, and it has been observed that *gregaria* Desert Locust hoppers migrate less persistently when isolated than when in bands (Fraenkel 1929, Kennedy 1939)

There is a need for more field and laboratory experiments on this point, using both hoppers and adults known to have had exactly the same history up to the moment of the experiment, and along the lines suggested by Gunn *et al* (1948, p 24)

As far as adults are concerned, there is some rather inconclusive additional evidence of a difference between the behaviour of migrants in swarms and migrants on their own During the summer of 1941 when swarms were seen by day emigrating westwards from the Anglo-Egyptian Sudan, numerous isolated yellow migrants were seen at Geneina, Darfur, flying west round the time of full moon in several successive months, and these individual flights were seen only at night (personal communication from Mr Bampfield, British Overseas Airways Corporation) Similarly, Predtechensky (1935*b*) observed isolated *gregaria* individuals flying high late at night, at a time when swarms were flying by day and settled at night

The evidence of gregarious behaviour in locusts seems to be conclusive, but it must be emphasized that migrants will fly steadily onward following parallel courses even when they are not subject to at any rate frequent stimulation from one another (p 194 and 195)

Gregarious reactions Mutual visual, olfactory, tactile, auditory, humidity and temperature reactions have all been suggested at one time or another as the basis of gregarious behaviour Humidity was suggested by Chauvin (1941) on very doubtful evidence, and seems most improbable not only because it is unspecific, but also because there is experimental evidence that *Locusta* hoppers collect in the driest places available, other things being equal (Kennedy 1937) Temperature, in the form of responses to the heat radiated from the sun-warmed black bodies of fellow-hoppers, was suggested by Shumakov (1940) as a possible aid to the formation of basking bands This seems more likely but has not been tested

Certain field observations on hoppers led de Lépiney (1933) to suggest olfactory responses were of considerable importance in band cohesion But Volkonsky (1942) stated that such responses, while important during gregarization, were reduced to a minor role or even disappeared when fully *gregaria* locusts had been produced Tactile responses, on the other hand, are plainly seen among roosting and basking adults, and in the jostling that goes on at times in both stationary and marching hopper bands as a number of authors have reported

None of these types of mutual stimulation can take us far toward understanding gregarious behaviour in migrating bands and swarms The air-borne stimuli, humidity and smell, could not explain the gregarious responses of hoppers to fellows down-wind of them, and could hardly produce responses as rapid and precise as those observed Thermal radiation and mechanical contact can affect only insects in very close proximity Auditory and visual stimuli seem to be the only ones which would be capable of producing gregarious responses with the rapidity and precision, and over the distances, observed among migrant locusts in the field

Observations and experiments in the field led Vayssière (1921) to suggest that locusts respond selectively to the air vibrations set up by their fellow-locusts, but seemingly clear evidence of this has been confused by contradictory field observations (Uvarov 1928, de Lepiney 1928, 1930, Williams 1933) In the laboratory, Pumphrey (1940) established the range of frequencies to which the tympanal organs of locusts respond, and their discriminatory responses to modulations of the basic frequencies He showed, moreover, that these paired organs are capable of discriminating the direction from which sounds come Later (in a private communication he has kindly allowed me to quote) he reported that the sound emitted by one flying locust evoked a definite response from the tympanal organs of another, and suggested that auditory reactions could serve as a means of maintaining swarm (and perhaps band) cohesion It is to be hoped these promising developments will be followed up by field experiments, for auditory reactions might play an important part not only in inter-attraction but also in mutual activation among swarm members, as well as making it easier to understand the cohesion of swarms migrating by night To man, there is, for example, an extended and dramatic swish of wings as the growing flocks of locusts sweep over at mass departure, and this sound might contribute toward bringing still-settled locusts into the air during the climactic last minutes of the swarm-launching process

On present evidence, however, first place among the agents of gregarious behaviour must be given to vision (Uvarov 1928, Kennedy 1939, Volkonsky 1942) Chauvin (1941) implies that the present writer (1939) regarded the visual attraction of hoppers to shrubs as the main evidence that the inter-attraction between hoppers was also visual That was only a minor point Evidence for the visual nature of inter-attraction comes from the sensitivity of locusts to all kinds of visual stimuli, especially movement, from the dense, sharp front shown by some marching bands, and from the speed and precision of the responses of one individual to another and their independence of air movement

Volkonsky (1942) satisfied himself that the inter-attraction of *gregaria* was visual, by field experiments which he did not, unfortunately, describe He attributed it to a

'réaction visuelle de reorientation qui consiste à ramener l'image d'individus freres dans la partie antérieure de l'œil composé'

He distinguished this reaction from the one responsible for parallel marching

'Une stimulation opto-motrice entre individus marchant parallèlement et qui ne persiste que tant qui l'image stimulante se trouve située dans la moitié anterieure de l'œil composé'

The cohesion of *gregaria* bands he attributed to the joint action of these two reactions

'Cette réaction visuelle de reorientation (particuliere à la phase grégaire) s'ajoutant à la stimulation opto-motrice reciproque (dejâ observee chez les *congregans*) permettrait d'expliquer la cohésion des bandes'

This dual conception of gregarious reactions is expressed most clearly in his interpretation of marching

'L'errance apparaît ainsi comme l'exteriorisation de stimulations motrices reciproques, contrebalancees par une inter-attraction des individus'

At first sight marching behaviour does certainly suggest there are two different reactions counter-balancing one another But on close examination it is difficult to see a clear distinction between them, what we observe are two forms of expression of a common underlying reaction The optomotor reaction is not, during marching, merely a means by which one insect makes another one move, it makes the other move in a certain direction, parallel with the first It helps to prevent scattering and is in this sense an agent of inter-attraction The present writer (1939, pp 525–6) suggested previously that there was no fundamental distinction between the reactions involved in inter-attraction and parallel movement, nor, indeed, between them and the attraction of non-migrating locusts to conspicuous objects (p 243) He would now add orientation to wind as another allied reaction All these reactions appear to rest on the common foundation of optomotor (visual compensatory) responses They differ in being evoked by different types and patterns of image movement and involve different forms and patterns of optomotor responses

Not only is the basic response common to these different types of reaction The different types of effective stimulus-situation involved also have something in common They all have something exceptional, outstanding or novel about them The reactions of an individual hopper to the movement of a man's arm show this same feature If he holds his arm out but stationary, or moves it very slowly, the insect is unaffected If he moves it more rapidly, the insect may pause and 'peer' at him If he moves it yet more rapidly, the insect hops wildly Similarly, in wind orientation, the insects do not make optomotor responses to *any* background image movement, such as the movement of images from front to back which is the normal and inevitable consequence of the insect's own movement The optomotor responses appear when the retinal velocity is novel in the sense of being a departure from that which the insect prefers In attraction to vegetation the insects do not turn toward *any* object along their path, 'à ramener l'image dans la partie antérieure de l'œil', but only toward *outstanding* objects like isolated shrubs

Among *moving* fellows, as in migrating hopper bands and flying swarms, the pattern of optomotor responses seems to be governed in much the same way as their pattern in wind is governed Image-movement from front to back at a moderate rate, as in the eyes of one locust overtaking its neighbour, evokes no compensatory response in the overtaker, it does not at once drop back to its previous position relative to its neighbour But when the neighbour is coming in the opposite direction, so that the image movement from front to back is at an excessively high rate, the locust does respond, by turning and following its neighbour, as seen during 'gregarious reversal' (p 229) Again, when the image-movement passes from back to front in the eye owing to being overtaken by a neighbour, this too is compensated, it is not a consequence of the locust's own exertions It provokes a powerful optomotor response, which gives the impression of an attempt to catch up with the intruder Back-to-front movement of background images owing to failure to make headway against wind seems to be compensated in much the same way, by an increase of pace

As far as the purely optical reactions are concerned, there seems to be no essential difference between those responsible for mutual attraction as seen most clearly during convergent movement into stationary bands, and those responsible for parallel movement in marching bands What differs in the two situations is the behaviour pattern shown by the band or swarm as a whole

When most of the hoppers are stationary, the neighbour-image-movement experienced by a moving hopper is due largely to its own movement The moving individual's compensatory responses to such image-movement bring the image concerned to the front of its eye, for only in that position will the image cease to shift about on the eye while the insect moves, as in what Kalmus (1937, 1949) has called photo-horotaxis Isolated hoppers are thereby directed into the main body from any point outside it When, on the contrary, the majority of insects are moving, the image-movement experienced by any one of them is due largely to the movements of its neighbours and not of itself A hopper making a compensatory response to the movement of a neighbour crossing its path must turn after, that is in pursuit of, its neighbour It may be left behind before becoming fully alined with its neighbour, and cease to respond to it It then pauses, or continues on its own course until it sees and responds to a newcomer, and so on

That sort of sequence is seen early in the launching process of a hopper band or adult swarm in the morning, or again when two bands or swarms meet at an angle But when a band or swarm has launched on migration, gross deviations between individual paths are less often seen The parallelism may then be due partly to the sun-compass-reaction But gregarious responses still appear wherever the insects are crowded and each individual is bombarded with stimuli from its neighbours Movements of one individual toward a neighbour seen on its flank, and so across the main direction of the mass, simply do not have time to develop The neighbour shoots ahead, followed by others, and the compensatory movement becomes a pursuit in line with the mass before it has developed into a traverse across the mass Forward movement in line with the mass, originating early in the launching process as a pursuit of neighbours, evolves into a preoccupation with simply keeping up with neighbours on either side in the fully migrating band or swarm Compensatory responses of this type perpetuate parallel movement and generate gregarious inertia

The continuing occurrence of active gregarious responses during the process of swarm migration shows itself in the abruptness of 'gregarious reversal' in wind (p 194) This term was applied to the remarkably well-synchronized change of course by members of dense swarms, from up-wind to down-wind in gusts and back to up-wind in lulls Its effect seemed to be to impose due down-wind courses on locusts which, when less dense, merely turned from up-wind to some across-wind course when hit by a gust Gregarious reversal seemed to depend on the fact that locusts losing headway or turning aside from their up-wind course began at once to drop backwards relative to their fellows still making headway into wind, thus stimulating the latter to turn down-wind after them until all were flying in parallel down-wind

The differences between the tracks of neighbouring fliers, which are here assumed to be the starting point for gregarious reversal in gusts, could come about in at least two ways First, it may be assumed that individuals differ in respect of the timing and strength of the responses governing their air speed and course Secondly, the tracks of individuals will differ also because the wind itself is not a smooth current, least of all during the onset of a gust This is apparent from the findings of Giblett (1932), who has been quoted already in part (p 207) to show that the large differences of velocity found in wind were unlikely to affect orientation Within these large 'eddies', however, there are much smaller eddies which produce rapid, *randomly* directed oscillations in a wind-vane Giblett writes (p 47)

> 'The wind-vane has a tendency to oscillate very decidedly at certain times and at others to remain much more steady A comparison of these points with the wind speed records show that the period of oscillation corresponds to a lull in the wind while the subsequent period of little oscillation corresponds to an increased velocity the decrease of oscillation occurred some 20 seconds after the increase of speed It would appear that during lulls in the wind and the initial stages of a gust there is a greater small-scale turbulence than after the establishment of the higher wind-speed '

Locusts meeting a gust would experience a sudden increase in turbulence, which would change the locusts' positions in relation to one another by disarranging their tracks, even if their courses were at first unaltered As an immediate consequence courses would also be thrown into confusion as each locust made compensation movements in response to the visible displacement of its neighbours The sharp turbulence is over in about 20 sec and the wind becomes smoother than it was before the gust, but remains stronger With locusts now facing in all directions and some therefore being carried down-wind past the eyes of others, and none able to progress due up-wind, a common down-wind course should be achieved rapidly

Confusion among fliers at the onset of a gust was often observed, as was to be expected from the meteorologists' results The confusion was greater among higher than among lower fliers The reason for this may well be that locusts flying above the maximum compensatory height have no means of 'correcting' their disordered orientations other than gregarious influence from lower fliers and the light-compass-reaction to the sun Fliers below the maximum compensatory height can readjust their orientation to the main wind direction quickly, between eddies or as they subside

The contribution of gregariousness to migration If gregariousness contributes to the impetus of the migrant swarm and is largely responsible for its cohesion and the parallel movement of its members, then it must be regarded as a very important component of migratory behaviour in swarming locusts We may reasonably infer that the migration of these insects would be less persistent, if they did not move in compact, 'disciplined' armies If they did not migrate in this way, be it noted, they would lose their uniquely catastrophic character as pests of crops

Their migration starts with the act of *mass departure* as it has been called, that is, when a large collection of insects not only start persistent flying at the same time, but all do so in the same direction and keep together in a group Whatever may influence it, mass departure is by its very nature a gregarious act, that is, it expresses a change in the relations between individuals The change is in the direction of closer inter-dependence, and this leads to that striking change in the movement pattern of the whole mass, called mass departure Mass departure is not a matter of individual behaviour

This point is stressed here because Gunn *et al* (1945, 1948) seem not to have taken it fully into account, although their study of the swarm launching process is the most thorough yet made In one place (1948, p 30) they did state that 'stream-away is essentially a mass phenomenon' Nevertheless, the conclusion they first drew (1945) from their study of the various factors that might affect the time of mass departure was that it was 'not due to a metabolic effect of the body temperature, once that is high enough, but is a *reaction* to air temperature' That is to say, the phenomenon was attributed to the direct action of temperature on individuals, rather than to an indirect effect, through the gregarious relations between individuals, on the movement-pattern of the mass

In the later, full account of their observations, Gunn *et al* (1948) granted that the air temperature might play a 'permissive' rather than a directly stimulating role in mass departure, but they left the whole question open, as a problem of balancing the quantitative importance of one factor against others, and said (p 44) 'gregariousness may not in itself be a causal factor in migration, though it may very well be a modifying factor ' If, however, it be conceded that mass departure is by its very nature a gregarious act, then gregariousness is thereby conceded to be a causal factor in swarm migration, and there is an *a priori* case for the role of temperature and of other external influences being in fact permissive (see also pp 236–238)

Each *gregaria* locust is an individual capable of independent activity and differing somewhat from its fellows in its responsiveness to external stimuli, including those from its fellows, and yet it is also a swarm member, capable of the closest integration into a larger unit of its fellows because its anatomy and physiology are such that it responds similarly to, and itself provides, the same types of stimuli as they do. The actual behaviour of an individual may be dominated by either one of these two sides of its nature, according to how much stimulation it is receiving from fellow-locusts And the gross movement-pattern shown by a mass of locusts depends on which tendency is uppermost in the individuals composing it Since other, extrinsic factors can influence the amount of stimulation the individual receives from its fellows, these factors exert a real, although indirect, effect on the gross movement-pattern shown by the mass

The whole launching process may be visualized in this light, on the working assumption that the air temperature acts permissively, through the internal temperature of the locusts, and in the following, necessarily rather schematic way

We start with a mere *assembly* of individuals, crowded but inert and in no immediate sense gregarious, which are then slowly brought into activity by the rising temperature Up to and through the phase of vol-planing and hopping flights the locusts' influence upon one another is limited almost entirely to mechanical contacts Flying locusts appear to have a negligible effect on other locusts resting or flying The fliers are too isolated and their flights too brief, and the others are not yet sufficiently responsive As fliers become more numerous and their flights lengthen, the movement pattern of the mass enters the 'milling' phase Obvious mutual stimulation, of resting locust by flier and of flier by flier, becomes quite frequent The locusts still behave mainly as independent individuals, but increasingly supply and respond to the specific stimuli which make them potential swarm members But as no more than two or three individuals are involved in any one exchange of stimuli and then only momentarily, they only deflect one another Directions generally are chaotic, hence the term 'milling'

As they get warmer more locusts fly and fliers stay in the air still longer, permitting gregarious and extrinsic orienting influences to create the rudiments of order The individual is now exposed to successions of stimuli from neighbours, and parallelism appears Groups are formed in the air, and gregarious re-alinement is increasingly of group by group, or of group by external agency (gregarious reversal in wind) We now have 'surging' But the groups are local and transient and follow divergent and inconstant directions Any given individual displays fully gregarious behaviour only in brief spells which are terminated when it flies out of its group, or when loss of heat to the air stops its flying and in that way cuts it off from the group While resting it reverts to its individual status, or regains a different form of gregarious status as a member of a basking group, more local and less fluid During milling and surging the whole mass of insects is more than an assembly, but less than a swarm, it is a *mob*

Eventually it becomes warm enough for locusts that take off to be able to fly on indefinitely A new situation now exists, for it has become possible for all the locusts in the mass to be in the air together Mass departure has become possible In this limited sense the rising temperature causes the mass departure But the newly created possibility of mass departure cannot be translated into actuality until all the locusts get into the air

In fact, as was mentioned, taking off does increase decidedly at this point There is no evidence for and no need to postulate any acceleration in the direct effect of temperature on taking off, or any nervous reaction to the air temperature occurring at this time but not before On the contrary, the break in the rising activity curve and the climax of mass departure can be brought about by an unbroken rise in temperature-regulated activity among physiologically quite heterogeneous insects, because there occurs a marked strengthening of the gregarious component in the behaviour of all the individuals in the mass

As soon as flights are no longer curtailed by the coolness of the air the number of fliers in the air rises steeply It would do so, owing to the lengthening of flights, even if the frequency of take-offs remained unchanged But, in addition, the growing masses of fliers in the air stimulate taking off by flock after flock of those still settled, until the entire mass is in the air The mass is now more or less continuous, the groups having fused Gregarious re-alinement can spread right through it This creates a common direction among all the individuals, with gregarious inertia now a property of the whole, gregariousness reaches its fullest expression This in turn leads to displacement of the whole The mass is no longer a mob It has become a swarm, and that, essentially, is what enables and obliges it to depart

To sum up gregariousness plays a significant part in migration, being one source of its 'momentum' Gregariousness affects also the direction of migration, by generating gregarious inertia This may be an important direction-stabilizing agency, especially if combined with a sun-compass-reaction

Air and body temperatures

Flight activity Much remains obscure concerning the effects of temperature on locust activity, but there is now enough information to form an opinion on the question of whether swarm migration is reflexly provoked or, in the main, merely released by it The question touches on the fundamental nature of migratory behaviour, and has been answered in both ways The suggestion that migration is provoked by temperature has been made at least twice, in different forms, flight being attributed at one time to over-heating, and more recently to a reflex acting through special air-temperature receptors

Hussein's (1937) laboratory work on temperature and locust activity led Uvarov (1937*a*, 1937*b*) at one time to the conclusion that

> 'Mass movements of hoppers and flights of adults, which are so characteristic of locusts, are not normal movements, but are caused by excessive temperatures These movements are definitely due to external factors and they continue only as long as the conditions remain unfavourable' (Uvarov 1937*b*, p iv)

Since then, Uvarov (1947, p 16) has taken up the opposite view

> 'As a rule, if temperatures are above a certain moderate level, gregarious locusts are more likely to be in flight than at rest Flying with them may be regarded as a normal state, and rest is enforced by environmental conditions '

The evidence undoubtedly favours this latter view, rest being presumably sometimes enforced not only by external but also by internal conditions Since Uvarov's 1937 statement was based directly on experimental facts, but his 1947 one appeared in an essay without the supporting data, it will be as well to give them here

Desert Locust hoppers cease marching at midday on hot days and come to rest in the coolest available situations (Fraenkel 1929, Predtechensky 1935*b*, Kennedy 1945) Marching starts, on the other hand, at 26° C according to Volkonsky (1942), or even 22° C according to Kennedy (1939), temperatures which are far from 'excessive' for these insects It is equally clear that adult migration does not require an 'unfavourable' temperature Bodenheimer (1929) put the limits for 'normal activity' of mature, *ph gregaria Schistocerca* adults in the laboratory at 20 and 42° C In his more precise study Hussein (1937) separated a 'normal activity' range between 23 and 36° C from a range of increasing 'nervousness' between 36 and 46° C The first flights by individual swarm members appear in the morning at body temperatures within and below Hussein's range of 'normal activity', as Gunn *et al* (1948, pp 16 and 39) have shown The taking-off observed at that time is by numerous, separate individuals scattered throughout the swarm (p 169), and it is most unlikely that the temperature threshold for it is much lowered by mutual stimulation Stimulation of one individual by others soon takes a hand, but is not a primary or a necessary condition for repeated taking-off

Mass flight cannot be regarded as spontaneous in the sense that isolated flights are, owing to the occurrence of mutual stimulation, and observations of isolated *gregaria* locusts *starting* on migration have not yet been recorded Hence it is at present impossible to say at what temperature migration would start without the aid of mutual stimulation Possibly the required temperature would be higher than for swarm migration But the fact remains that Volkonsky (1939) found that the threshold body temperature for mass taking-off by locusts in a large cage varied between 31 and 37° C, and Gunn *et al* (1948) found that the *highest* body temperatures recorded at stream-away in the field varied between 27 and 41° C on different occasions That is to say the start of mass migration often occurs when the locusts' body temperatures are well within Hussein's range for normal activity Waloff's (1946) finding that the flight activity of Desert Locust swarms in East Africa remained at a high level as long as the average *maximum* temperature was above 20 to 22° C (cp Predtechensky, 1935) was strikingly paralleled by the finding of Gunn *et al* that mass departure occurred at air temperatures between 17 and 23° C

Mass migration is not caused, therefore, by excessive temperatures On the contrary, Volkonsky (1939) found that his caged swarm ceased taking-off when body temperatures reached 45° C This contrasts sharply with Hussein's laboratory observations, in which 45° C was the temperature at which 'nervousness' passed into 'excitement' In the field, Olsuf'ev (1930) found a swarm of *Locusta migratoria migratoria* settled at midday at a screen temperature of 35° C and remarked on the difficulty of making the locusts fly, they migrated only when the temperature was below 30° C Similarly, Predtechensky (1935*b*) found that young swarms of *Schistocerca* in Turkestan rested in shady positions during the daytime when the air temperature reached 35° C, and did not take off until it fell again to 30° C in the evening, and Bodenheimer (1944) records a midday lull separating morning and afternoon periods of migratory activity by *Dociostaurus maroccanus* Telenga (1930) did observe a *Schistocerca* swarm taking off at midday at a temperature which must be regarded as excessive These locusts were resting on the ground, apparently owing to the very hot weather, for most of the morning, and were driven finally to take off only when the air temperature reached 40 to 42° C, so that this seems to be an exceptional case During the present observations adult migrants were not seen resting on the ground at high temperatures, and fledglings were observed migrating, although interruptedly, throughout days when the maximum screen temperature reached 40° C But older locusts were seen, during the heat of the day on such very hot days, to accumulate at a high and presumably cooler air level where they merely circled about, so that they had effectively ceased migration even without settling

The immobilizing effect of high temperature probably explains why swarms have been reported to fly at night instead of by day in hot weather Night flying is of course difficult to observe, and is probably more common than the literature suggests Regnier (1931) reported that swarms migrated at night in Morocco when the air temperature was over 27° C Captain A Lea (unpublished observations kindly supplied by the Anti-Locust Research Centre), working in Tripolitania in June–July 1944, and finding the young swarms of *Schistocerca* disappearing from the coastal districts and reappearing farther south, although they were seldom seen in flight during the day, concluded that most of the migration was occurring during the hot nights Observers in Algeria (1929) come to a similar conclusion during the southward migration of 1929 And Rao (1942) writes 'In the summer months it is probable that migration takes place in the evening or early part of the night, while in the autumn months and in winter the nights are cold and movements probably occur during mid-day or early afternoon ' The context is not quite clear, but Rao appears to be referring here to both phases, solitary and gregarious

The contradiction between these field observations, showing maximum flight activity at moderate temperatures, and the laboratory results of Bodenheimer (1929), Parker (1930) and Hussein (1937) showing maximum activity at excessive temperatures, is merely apparent We now know that the old idea of a simple, direct relationship between temperature and activity is entirely misleading

From the laboratory side it has been shown that activity is a complex phenomenon, and cannot be measured physiologically, say by the oxygen consumption or rate of locomotion of such animals as are found moving at any chosen moment (Nicholson on *Lucilia cuprina*, 1934, Gunn & Hopf on *Ptinus tectus*, 1942, Fraenkel & Gunn 1940) If we measure the amount of activity, e g by the ratio of moving to resting animals, rather than the rate of locomotion, we find the shape of the temperature-activity curve varies according to the rate of change of temperature When the temperature changes very slowly, or, what amounts to the same thing, when insects are exposed for long periods to a series of constant temperatures, the maximum activity occurs at an *intermediate* temperature, nearer to that of cold stupor than of heat stupor, which it seems legitimate to call the *optimum* temperature for the insect from a behavioural point of view When the temperature is rising slowly in the laboratory, activity at a lower temperature than this optimum surpasses the level reached after a long stay at the optimum With further rise of temperature, activity falls below the level found after a long stay at the optimum Activity rises again only after a considerable further rise in temperature, but now steeply, to the 'frenzy' just preceding heat stupor The different curves seem to reflect the varying interference by nervous reactions to temperature *changes*, against the background of the direct 'metabolic' or 'releasing' effect of temperature

Laboratory studies on temperature and locust activity could not have revealed any similar effects because the activity was not measured quantitatively Bodenheimer (1929), Parker (1930) and Hussein (1937) graded activity on an arbitrary scale without taking note of the proportion of individuals in motion at any given moment From their accounts one might think there was a simple, direct relation between activity and temperature That seems to be the origin of the idea that mass migration, which is activity of a very intense kind, must be caused by excessive temperatures This idea derived some support from the behaviour of locusts in temperature gradients There they collect at moderate, intermediate temperatures and do so partly because they come to rest, that is, are less active there But behaviour in a temperature gradient, too, depends on its steepness, that is on the rate of change of temperature to which the insects are subjected as they move along the gradient Activity levels at various temperatures in a given gradient have no universal application While information on the temperature-activity relations of locusts remains incomplete, it has at any rate been shown that very rapid temperature changes have not a direct, but an inverse ortho-kinetic effect, a fall of temperature provokes movement and a rise stops it, over the range of moderate temperatures (Kennedy 1939) Some further information is available concerning another kind of activity, feeding, in *Schistocerca gregaria* Husain, Mathur & Roonwal (1949) found that the amount of food consumed per day was at a maximum between 33 and 37° C, falling off at lower *and higher* temperatures, the maximum rate of development being at about the same intermediate temperature

If maximum activity were to occur at excessive temperatures, as a fixed law, that would imply that activity itself was something 'abnormal', imposed on the animal directly from outside, and that complete inactivity was the normal state In fact, complete inactivity is abnormal behaviour for locusts In the field the maximum *sustained* activity occurs at moderate temperatures, as it might also, judging from the work on other insects, under appropriately arranged laboratory conditions

Inasmuch as they show maximum activity at moderate, and minimum activity at excessive temperatures, migrants in the field behave in a way that corresponds with the behaviour of non-migrants Thus Volkonsky (1942) coined the expressive term 'euthermy', defined as the external conditions (the range of available temperatures) permitting non-migrant locusts to maintain their body temperature at the preferred level He showed that in such conditions individual *congregans* hoppers of *Schistocerca gregaria* wandered freely within the habitat, which they did not do at lower *or higher* temperatures The amount of undisturbed activity among various non-migrant *solitaria* or *congregans* populations of the same species observed by the writer (1939), appeared to decrease after the insects had come down to the ground in the morning, increased again as the morning basking period progressed, and then decreased still further when 'basking-places' became so hot that the insects retired to the shade On cloudy, winter days when the screen maximum did not reach 30° C the period of basking and wandering freely continued right through the day On cloudless, spring days when the maximum exceeded 30° C such activity gave way to almost complete inactivity during the hot midday hours—except for occasional individuals which emerged on to open ground and became at once violently active until they regained the shade Similarly, the activity of a number of species of non-swarming Acrididae on a sand-dune in Palestine (Bodenheimer 1935) decreased steadily after reaching a maximum when the soil surface temperature was about 35° C In consequence, diurnal activity showed a single, midday maximum in spring and autumn, but two maxima separated by a midday lull in summer This fact is familiar to collectors, and was justly emphasized by Rao (1942) in connexion with the estimation of locust populations in the field

The difference between migrant and non-migrant locusts, therefore, is not that migrants are provoked into mass movement by excessive temperatures which non-migrants somehow escape Both are most active over a period (that is 'spontaneously' active, apart from immediate reactions to more or less sudden temperature changes) at temperatures that are optimal, not unfavourable for them Migrants and non-migrants differ rather in the intensity of their normal activity at moderate temperatures And if migratory flying is the normal activity of *gregaria* locusts when at or near their preferred temperature, which is the temperature to which their various temperature reactions tend to return them, then those reactions will also conspire to keep the insects flying 'automatically', as Shumakov (1940) suggested with regard to the marching of hoppers Since Gunn *et al* (1948) recorded body temperatures ranging up to 41° C at the time of mass stream-away, it may well be that migrating locusts often have body temperatures within the range where activity has ceased to be 'normal' and has become slightly 'nervous', for nervousness begins at about 36° C on Hussein's scale On this scale, in fact, gregarious locusts are somewhat nervous even at the temperature preferred by them, 40 to 42° C, and if they tend to keep to that temperature not only in the laboratory but also, as seems probable, in flight, then migrants must be habitually somewhat nervous In this sense, Hussein may have been quite correct in saying that adults in full flight are not behaving normally That is a very different thing from saying that migration is abnormal in the sense of being caused by temperatures that are excessive, i e well above the preferred temperature If migrants spend most of their time in a state of slight 'nervousness' that is due to their own exertions, released by temperatures below those causing nervousness When they reach Hussein's 'excitement' temperature, migration tends to stop If the slight nervousness of migrating locusts is to be classed as an abnormal condition, then it can only be said that it is normal for *gregaria* locusts to behave abnormally It is the insects themselves that are 'abnormal', which is simply another way of saying that migrants are insects with a peculiar physiological constitution

These conclusions accord with Uvarov's (1928) original views to which he has since returned, but the theory that migration is provoked rather than released by temperature has recently been revived by Gunn *et al* (1945)

> 'Locusts will not fly if the body temperature is too low It appears that mass departure is not due, however, to a *metabolic* effect of the body temperature, once that is high enough, but is a *reaction* to air temperature '

The other possibility, that the air temperature might act 'permissively' in bringing about mass departure, was discussed in Gunn *et al* later paper (1948), but considered on the whole less likely than their original suggestion

> 'Apart from the effect of radiation, the factors affecting the difference between body temperature and air temperature will depend directly or indirectly on the energy of flight It is conceivable that the interrelations between them will be such as to result, once a steady state is reached, in a relatively constant excess of body temperature over air temperature, and that the fundamental constancy at stream-away is the body temperature of locusts which have been flying for long enough to reach this steady state The complexity of the interrelations makes this somewhat improbable. Alternatively it may be that the relative isolation of superficial parts like the antennae will bring them close to air tempera-

ture A reaction to air temperature through receptors on such appendages would then be consistent with the field observations' (1948, p 38)

Let us examine the argument here, for the question is of fundamental importance If the hypothesis of a nervous reaction to temperature causing mass departure were well founded, it would lead to the rather unexpected conclusion that the overriding behavioural characteristic of gregarious locusts, persistent migration, was not an outcome of their general physiological make-up, but was due, in essence, to one special reflex peculiar to them The question may be considered in two parts first, why mass stream-away should be considered a reaction to *air temperature*, and secondly, why it should be considered a nervous reaction at all

The reasons for emphasizing air temperature as against body temperature were

> 'The most consistent data were for air temperature, this was 17–23° C (average, 20° C) at the beginning of stream-away '
>
> 'Careful consideration of body temperature data reveals no consistent relation between them and stream-away, except that body temperature was always above the permissive temperature for flight (20° C) at stream-away The warmest locusts caught ranged from 27 to 41° C at that time on different days' (1948, pp 5, 6)

The suggested explanation of stream-away in terms of a nervous reaction to temperature (1948, p 38, and quoted above) came as the conclusion of a discussion opened thus

> 'This fact, that stream-away is comparatively independent of the body temperatures which we recorded is unexpected and requires explanation' (1948, p 30)

However, on the previous page the method of recording body temperatures was described in detail, and this is referred to in the summary on p 6

> 'Since stream-away occurs as a result of sustained flight, as distinct from the short flights commonly seen earlier in the day, and since representative body temperatures from locusts in sustained flight could not be obtained, it remains possible that there is a relation between body temperature in flight and stream-away '

Since the recorded body temperatures were not those of locusts that had been flying long enough to have reached thermal equilibrium with the air, it is not after all unexpected that they varied much more widely than did the air temperatures recorded at the time of mass departure These data do not seem to provide any evidence against the body temperature being the deciding quantity for stream-away

As to whether mass departure is a reaction at all Gunn *et al* (1948) point out (p 31) that 'locusts do not simply take-off when a certain body temperature has been reached', and they go on to say (p 33)

> 'This conclusion suggests that the assumption of upward flight, as a preliminary to stream-away, is a behaviour reaction, the stimulus for which can hardly be body temperature, because of the great range of maximum body temperatures when it occurs '

Taking-off may, indeed, occur only in response to some trigger stimulus and probably does so in response to many kinds of stimuli But such triggering-off occurs repeatedly *before* mass departure, it is not what is new at that time

'Using an old terminology, the short flights made by many locusts before stream-away would be called *trial* flights, which are repeated as long as the conditions for take-off are adequate, until more continuous flying occurs as soon as the conditions in mid-air are appropriate for staying up' (p 38).

When one is considering taking-off, which is a dramatic change in *individual* behaviour, it is natural to think in terms of reactions, but the mass departure depends, as far as the individual is concerned, on the mere continuation, in place of the previously repeated cessation, of an activity, flight, which was already in train, and which is destined sometimes to continue for many hours This does not suggest a reaction at all

The idea of a reaction would not have arisen, it appears, were it not for the fact that mass departure starts, as a rule, rather suddenly, as the only obvious break in the morning sequence of movement-patterns The main object of Gunn *et al* was not to make a causal analysis of the process by which a swarm becomes finally launched on migration, but rather to find what governed the timing of this process They considered the density of the locusts as likely to govern the intensity of gregarious excitation, and in that sense as a factor comparable with other regulating factors which vary from time to time and place to place, like temperature humidity, wind, etc And among these, the factorial analysis pointed to air temperature as the most important influence setting the time when flying about passed over into stream-away

So far the argument is straightforward, but at this point it makes a leap, with the suggestion that the air temperature may not merely determine the *time* of mass departure, but be its direct cause, through a nervous reaction This is a different proposition altogether, not supported by the observations and at variance with the authors' statement (p 30) that 'stream-away is essentially a mass phenomenon' It is also at variance with their suggestion (p 24) that 'the unity both of flight activity and of orientation observed at stream-away might be due to mutual stimulation' If these statements are correct, then the main reason for postulating a nervous reaction as the cause of mass departure is removed Unity of flight and of orientation are themselves the direct cause of mass departure, as discussed elsewhere (pp 230–232)

The suddenness of mass departure appears to come from a sudden change in the movement-pattern within the mass, which occurs automatically when mutual stimulation between individuals reaches a certain intensity Such a change, dramatic though it often is, requires only a small quantitative increase in the same 'permissive' action that temperature had been exerting before the mass departure It does not require a new type of temperature effect, a nervous reaction, to come suddenly into play

The persistent flying observed among gregarious Desert Locusts, we may conclude, is a characteristic of the insects themselves, as near to being truly spontaneous as any so-called spontaneous behaviour Temperature may be one among a number of stimuli which provoke *taking-off*, but its most important role in mass migration seems to be that of a releaser, permitting locusts that have taken off to stay warm enough to fly on

Height of flight Waloff (1946*b*) and Rainey & Waloff (1948) have produced some direct and more circumstantial evidence that Desert Locusts reach considerable heights with the aid of thermal up-currents On this assumption and in the light of an analysis of the meteorological data, they were able to work out, with an impressive degree of plausibility, how certain long-range swarm movements over the sea could have been brought about Swarms are sometimes seen pillaring upwards rather like cumulus clouds, in a way that suggests the locusts are in fact at the mercy of strong thermal convection Such convection requires strong solar radiation to heat the ground, and it would seem to follow that locusts would be found flying higher, on the average, in sunny than in cloudy weather, and so higher in the hot dry seasons than in the rainy seasons

The evidence of such an effect of temperature on the height of flight is so far fragmentary Regnier (1931) observed swarms of *Schistocerca gregaria* rising vertically during the warmest part of the day, an act which enabled them to cross the Atlas Mountains Bruzzone (1936), who claims to have kept a single swarm of *S cancellata* Serville (=*paranensis* Burmeister) under continuous observation during a whole month, stated that the greater strength of the sun the higher rose the swarm A similar impression was formed during the present studies

It was decidedly warmer and sunnier during the Iranian observations than during the Kenya ones In Iran locusts were seen flying at more than 30 m on fourteen occasions (43%) and at more than 100 m on six of the total of thirty-one occasions quoted in table 2 In Kenya they were seen flying at more than 30 m on only four occasions (25%), and at more than 100 m on two out of the total of sixteen occasions quoted in table 2 There were four other occasions when locusts were seen very high (more than 100 m) two in Arabia (table 2, nos 1 and 3), and two when the swarm in question had been engaged in mating and egg-laying, in Iran on 1 June 1943 and in Kenya on 22 April 1944 There were, therefore, twelve occasions altogether when locusts were seen flying very high, and on all but one of these it was remarked that the weather was unusually hot The exception was on 27 June 1944 (table 2, no 49) when the swarm reached 200 m as early as 09 00 hr , but this was the swarm which had been repeatedly activated by low-flying aircraft

On eight of the other eleven occasions the high-fliers were not moving in a common direction but milling about, and on six out of these eight occasions the very high-fliers occurred as scattered individuals and were either separated by a considerable gap from locusts at lower levels (nos 20 and 21 in table 2, and mating swarms on 1 June 1943 and 22 April 1944), or occurred in the complete absence of lower locusts (nos 15 and 30 in table 2) The high-fliers in these six cases were only just visible to the naked eye when the sun caught their wings They appeared and disappeared between the observer and the sun in a way that indicated they must have been present, if invisible, over a large expanse of sky They extended upwards as far as could be seen even through glasses These six cases of very high circling flight all occurred when it was extremely hot and thermal up-currents were frequent, often in the form of violent 'dust-devils'

Since the height at which the insects fly can make a great difference to the direction and speed of their movement over the ground, it is an urgent matter to obtain more data on the effects of temperature, and especially of radiation and convection, on the height of flight But it should be borne in mind that when locusts rise in hot weather, this may not be merely because they are lifted passively by the rising air Rising might be to some extent a reaction to temperature, one of the locusts' means of regulating their body temperature and keeping it near the preferred level (cp p 241) Even when the mechanical lift is mainly due to the rising air rather than to active climbing flight, the locust's act of permitting the air to lift it in this way cannot be regarded as an entirely passive matter, the locust might, for example, settle, if too hot, rather than remain air-borne

Direction of flight Several authors have attributed changes of direction by flying swarms to supposed changes of air temperature Thus, Regnier (1931) observed a swarm of *S gregaria* arriving at Rabat (Morocco) with a hot wind from the south-east Upon reaching the sea-shore, it turned and flew along the coast All swarms observed during several months turned along the coast-line in this way He suggested that the change of direction was induced by the encounter with the supposedly cool air over the ocean Bruzzone (1936) describes a swarm of *S cancellata* Serville encountering a cool southerly wind and turning on itself with a period of much confusion during which the locusts in front were turning and meeting others still coming up before meeting the cool air Later, the same swarm, flying northwards, encountered currents of cool air descending from some hills, turned west, and passed through a gap between the hills Both changes of direction Buzzone attributes to the drop in air temperature Predtechensky (1935*a*) made similar observations in Iran in 1929–30, for he concluded (in somewhat confusing terms) 'meeting with cold air media, locusts endeavour to escape their influence, by directing their flights toward a warmer stratum of air' (Mr Koffler's translation, 1938, p 70) There are also various reports, quoted on pp 202–208, of swarms changing direction on encountering, and flying with, the wind in front of storms

In most of these cases it is possible that a sudden change of air temperature contributed to the observed change of direction, but nothing more definite can be said for other changes in conditions, such as the speed and structure of the wind, occurred at the same time It is fairly safe to assume that horizontal air-temperature gradients are too irregular or too gentle to permit the *continued* kind of directed temperature reaction implied by Predtechensky in the quotation above Even on the ground, where steep gradients do exist among vegetation, directed temperature reactions did not appear to play much part in the behaviour of locusts (Kennedy 1939) The changes of direction at the sea-shore reported by Regnier (1931) and on p 198 could have been visual responses to the changed ground pattern (see p 208), and it seems very doubtful whether any but the lowest-flying locusts would feel a change of temperature at the moment of meeting the shore-line in an off-shore wind

On the whole, evidence of a direct influence of temperature on the direction of flight is inconsiderable and unconvincing

The sun as a directing influence

There is no evidence that the direction of swarm flight bears a consistent relation to the direction of the sun and no one has suggested this De Lépiney (1928) is the only observer who has been convinced that flying swarms were oriented by the sun, for he observed numerous cases of courses being toward it, although tracks were not necessarily toward it, being deflected by the wind But even he said that such orientation occurred only sometimes

It would be unwise, however, to neglect the possibility that migrants do orient to the sun, merely because their observed orientation to it is variable or because other influences, notably wind, seem to have a more important orienting action Thanks to the work of Grassé (1922, 1923), Fraenkel (1929, 1930), Volkonsky (1939) and others a number of orientation reactions to both radiant heat and light have been established in locusts in the laboratory Only further work can decide to what extent these reactions occur during migratory flying, but it is improbable that they do not occur at all

De Lépiney drew a parallel between his observations of swarms flying toward the sun and his own and Grassé's laboratory experiments showing positive phototaxis and thermotaxis As far as the heat reaction is concerned, the parallel may not be valid because, in the laboratory, the radiant heat source was close to the insects which were therefore moving in a gradient of radiant heat intensity and perhaps of air temperature also, and may have been directing themselves along these gradients With the heat source as remote as the sun, however, no such gradients exist, so that if the fliers were indeed reacting to the sun's radiant heat, the reaction was not necessarily equivalent to the positive thermotaxis seen in the laboratory Phototaxis, on the other hand, could occur to the sun as to an artificial light in the laboratory

It happens that the orientation reactions of locusts to radiant heat and light have been worked out more fully for resting ('basking') locusts than for walking or flying ones These reactions involve perpendicular orientation to both heat and light rays when the locusts are below, and parallel orientation to the rays when they are above, their preferred temperature, about 40° C (Volkonsky 1939) These reactions form a part of the locust's system of regulating its body temperature—a function presumably as necessary in flight as on the ground

Two different methods of body-temperature regulation are known in locusts changing the orientation to heat rays, and moving to a cooler situation Flying locusts must often be in danger of overstepping their preferred temperature (see p 236), and may be more dependent on changing their body orientation as a means of temperature regulation than are locusts on the ground The other method of temperature regulation would be less effective in flight than on the ground, because cooler situations are less immediately to hand in the air If the locusts de Lépiney observed flying toward the sun were reacting to it as basking locusts do, their parallel orientation to its rays would indicate that they would have been above their preferred temperature in any other orientation Their flight toward the sun would therefore be in no way comparable with the movement toward the heated plate in the laboratory, for there, when the locusts became too hot, they walked away from, not toward the plate

It has been suggested that the direction in which hoppers start marching may be perpendicular or parallel to the sun's rays according to their basking orientation at the time (Kennedy 1945) Since the wind is often very weak in the morning and appears to have an important orienting influence on adults when it strengthens later, morning might be the best time to look for the basking type of orientation to heat and light rays among the adults also Gunn *et al* (1940) concluded that their data gave no support to the idea of parallel orientation to the sun's rays at stream-away, but that it was possible orientation was often at right angles to the rays That would be expected if the locusts streamed away while still below their preferred temperature, which the body-temperature measurements suggested they usually were More data are required on orientations not only at stream-away but also before it, when changes of orientation might be particularly revealing The four observations on the morning behaviour of migrant swarms recorded here (figure 1, p 171) included some such data but are too few for further consideration at the present Thus while there is so far no evidence that orientation reactions of the basking type occur in flight, they might be worth looking for, especially when temperatures are very low or very high and wind orientation is unlikely

Quite apart from their 'basking' orientation reactions to radiant heat and light, locusts are known to be positively phototactic up to their preferred temperature, under certain conditions (Volkonsky 1939, Kennedy 1939, pp 491–494) The positive phototaxis is rather easily suppressed by other reactions While resting, adults will orient perpendicularly to 'cold' light rays But they change their orientation to one parallel with the light rays just prior to making a move, and so walk or fly *toward* the light (Kennedy 1939, p 450) There is nothing in Volkonsky's account (1939) nor the writer's (1939), to rule out the appearance of positive phototaxis at any light intensity and any body temperature, provided there is no overriding reaction to radiant heat, wind, etc Locusts taking off after sunset appeared to be reacting in this way when they flew predominantly toward the light western sky (p 175) as was observed also in solitaries (Kennedy 1939, p 450)

Otherwise, however, there is as yet no evidence that phototaxis has an important influence on the direction of migration, for there is an alternative explanation of Lepiney's examples of flight toward the sun, in terms of the basking type of parallel orientation to the heat and light rays

While there is no satisfactory evidence that the sun has any *lasting* orienting influence on hoppers or adults, there is good evidence, as far as hoppers are concerned, that it has a temporary, direction-stabilizing influence, through the sun-compass reaction

As seen in other insects, a light-compass reaction is one in which the insect moves at a constant angle to a light source, but an angle that is not laid down permanently (Fraenkel & Gunn 1940) It might be called a 'temporary fixation reaction' The points on the eye at which the light is 'fixed' are not limited to one or two, depending on the body temperature, as in the true light-fixation reaction described by Volkonsky (1939) as part of the locust basking-reaction complex Instead, any point at which the light has been held for some time becomes the fixation-point at which the insect itself then holds the light by means of compensatory turning movements made in response to any subsequent shift in the position of the image Such a reaction, in respect of the sun, has been demonstrated in marching hoppers (Kennedy 1945)

Direct evidence of the same kind is still awaited for flying adults Although it did prove possible to make temporarily shaded fliers reverse their direction by throwing the sun's reflexion on to them from the side opposite to that on which the real sun had been shining, only five individuals were so treated, and they emerged too quickly from the shade (p 196) But, unless we are to postulate an innate sense of direction beyond the reach of experimental investigation, we are obliged to find an external cause for the notable degree of stability of orientation observed among migrants when temporarily deflected by the wind or by moving or stationary obstacles (pp 196 and 197). However important compensatory reactions to wind may be, locusts do not follow every little shift in the wind direction even when their tracks are deflected, and they quickly revert to their previous course after temporary changes of course due to sporadic wind gusts or to obstacles, even when isolated from other locusts The sun, acting through a compass reaction, is at present the only external cause that seems not only possible but probable in such cases Once again, more observations and experiments are called for, especially when the sun is obscured

Assuming as a working hypothesis that the sun-compass reaction does occur in adults, the direction-stabilizing capacity of this reaction is obvious It could make a primary directing influence like the wind even more effective than it otherwise would be in preserving the uni-directional character of migratory flight, for full weight would thereby be given to the mean wind direction while the disruptive effect of temporary wind shifts was reduced to a minimum When locusts then encounter a temporary cross-wind, the tendency to turn into the new up-wind orientation is resisted, just as diversionary attempts by man are resisted, and a temporary compromise seems to be reached between an up-wind orientation and the old, previously established one This is illustrated in figure 8 and is also described, although otherwise interpreted, by Williams (1933, 1942)

Again, if a locust had 'fixed' the sun's position in its eye while close to the ground, and then rose, it would be able to continue in the same up-wind orientation when too high to react to apparent ground movement There is commonly much internal circulation in flying swarms, upper and lower fliers changing places from time to time Orientations could be then corrected with respect to the wind during approaches to the ground and retained during excursions to higher levels

When the wind is negligible near the ground, or in any wind at heights where apparent ground movement is too slow to provoke orientation responses, the light-compass reaction to the sun could become of first importance It and 'gregarious inertia' (p 194) could then serve as continuously acting, *complementary* orienting influences, as has been described for marching hoppers (Kennedy 1945) But it is emphasized that neither of these reactions could originate an orientation with respect to the ground They serve only to stabilize and perpetuate courses set by other means They cannot therefore explain the geographical trends in migration

Landscape

Field observations of hoppers (Kennedy 1945, Chauvin 1947) strongly suggest that features of the terrain over which they are migrating influence their direction above all visually This is still more probable for adults which migrate out of mechanical contact with the ground This section is therefore headed not 'Terrain', but 'Landscape'.

Avoidance of obstacles Deft avoidance of obstacles is one of the characteristic features of migrant behaviour (p 197) Migrants approaching an object in the line of flight change direction before reaching it, fly round or over it and resume their previous direction as soon as the object—tree, man, or whatever it may be—has been circumvented We are not concerned here with the resumption of the previous direction, which is attributable to the sun-compass or some other direction-stabilizing reactions, but with the change of direction on approach to the object Such obstacle-avoidance is the migrant's repeated, typical reaction to conspicuous objects, even stationary ones, whereas non-migrant locusts, when not actually being chased by conspicuous 'objects', are often seen to direct themselves toward and settle on them (p 199) Such positive attraction appears among migrating locusts only when migration is ceasing, as in the evening when the whole swarm will soon be settled It seems, therefore, that migrants in full flight are in a peculiar 'mood' or state of reactivity, which disappears as soon as steady migration flying ceases, or it might be more accurate to say that migration ceases because the 'mood' disappears. A fully comparable state of affairs was found in hoppers While on the march they also circumvent or surmount obstacles and retain a constant direction by means of their sun-compass reaction and gregariousness despite temporary deviations, but as soon as marching slackens they lose their common direction and are attracted to and settle on conspicuous objects (Kennedy 1945)

The visual nature of obstacle-avoidance was especially clear in the black cloth experiments (pp 197–198) The cloth was no real obstacle in the mechanical sense, but only a novel and striking feature, appearing suddenly in the locusts' field of view The essence of the locusts' reaction was a change of direction away from a suddenly appearing, conspicuous, visual feature The cloth was, of course, a very small, quickly passed feature at most To appreciate the significance of the reaction one must consider what would happen if the novel feature were far bigger In that case it would cut across a large part of the insect's retina, and would persist in doing so for a time despite the insect's progression Here again it is useful to consider hoppers (Kennedy 1945) in which comparable behaviour was observed, but in convenient miniature, since their rate of locomotion and field of view on the ground are restricted On encountering a new vista, whether a suddenly appearing large obstruction, or at the brink of water, or at a precipice, they paused, 'peered' and then, sometimes after a phase of confused pottering about, turned and moved along parallel with the brink of the visual obstacle Adults might be expected to behave similarly in relation to physical features of suitable size, which recalls Regnier's (1931) and other observations of swarms that changed direction upon reaching the sea-shore and flew thereafter along the shore-line (pp 198 and 240) It seems much more likely that the locusts were reacting to the sight of the sea than to a change of temperature such as Regnier suggested Thus the evidence lends substance to Rao's (1942) suggestion that 'migratory flights are presumably halted by a sight of the great barrier of the sea'

Locust swarms do often cross the sea despite the above evidence that they sometimes turn aside rather than leave the land If the avoidance be visual, it is not difficult to imagine conditions under which it would not occur, for instance with locusts that were high, or where the shore-line was not conspicuous

Once a new direction parallel with the visual obstacle's border was assumed, it was persisted in by both hoppers and adults Hoppers moved along parallel with lateral 'walls', whether of water, earth or shrubs, following every bend (Kennedy 1945), even when the hoppers concerned were out of sight of one another so that mutual vision was ruled out as a guiding factor They did not have their direction corrected repeatedly by physical encounters with the 'wall' Evidently they were keeping alined with it by visual means

Chauvin (1947) made a revealing observation in this connexion Writing of obstacle-circumvention by marching *Dociostaurus maroccanus* hoppers, he says

> 'Lorsque l'obstacle laisse une ouverture médiane de 15 centimètres au minimum, les Criquets ne cherchent plus à le contourner mais s'engouffrent en masse par l'ouverture '

This parallels the behaviour of a *Schistocerca* swarm already described (p 198), which turned to stream through a gap in an escarpment, thereby resuming the direction it had been following before being diverted along the escarpment a few minutes earlier To quote Chauvin further

> 'Un obstacle allongé parallèle à la direction générale paraît sans aucun effet, même s'il porte une overture de 15 ou 30 centimètres de large, mais à condition que la voie soit libre de part et d'autre'

Such failure to respond to openings in a wall paralleling the established direction of movement, so long as the way ahead lay open, was observed many times also in Desert Locust hoppers The statement (Kennedy 1945, p 256) that hoppers 'continued, as they moved along, to keep at an approximately fixed distance from the walls by visual means' was misleading in so far as it implied that the hoppers were constantly responding to visual stimulation from the side Chauvin's observations show that it is to gross changes in its *forward* field of view that the insect is primarily responding in such cases, by turning in the face of an obstruction but moving straight ahead as long as the way ahead lies open Similar behaviour is said to guide young turtles down to the sea from their hatching sites on the shore (Parker 1922)

This is not *phototactic* behaviour, however, in locusts The increase in illumination from in front experienced upon reaching the edge of a precipice, or of water, had the same arresting and deflecting effect on the hopper as had the decrease of forward illumination experienced upon coming up against a dark, upstanding obstacle The reaction is to some gross change in the anterior field of view, not to illumination as such Thus the responses concerned in obstacle-circumvention and, equally, those concerned in rectilinear movement along rectilinear features of the visible environment, constitute yet another type of visual compensatory reaction, in this case to changes in the anterior field of view The reaction is another special case of the general tendency of migrating locusts to 'keep their visible environment as constant as is compatible with their own continued movement' (Kennedy 1945) Greater or smaller changes in the lateral field of view are an inevitable accompaniment of continued movement They are produced by objects which are not in the direct path of the insect and so not incompatible with its continued movement But objects in the direct path of the insect are often physically incompatible with its continued movement and, physically or merely sensorily incompatible, they do in fact provoke active compensatory responses having the effect of restoring to the anterior field of view the general character to which the moving insect has become accustomed If this be true of hoppers, then we should expect to find adult migrants behaving with relation to a 'wall' on land much as do hoppers, although on a larger scale Such behaviour is in fact well known the tendency of swarms to move along valleys This was observed generally in mountainous Iran apart from the particular instances given above, and has been mentioned by other authors (Predtechensky 1935*a*, Zolotarevsky 1930, Vosseler 1905) Other factors are probably involved, wind and temperature especially, but this tendency is at least consistent with the principle of 'movement in the direction of maximum constancy of the visual field' (Kennedy 1945) Again, more experimental work is needed on adults

Attraction to conspicuous objects Previous work has shown that both hoppers and adults are attracted to conspicuous objects in their vicinity (de Lépiney 1928, Predtechensky 1935*b*, Bodenheimer 1944, Kennedy 1939, 1945) This attraction seems to be similar in principle to the attraction of non-migrating *gregaria* hoppers to one another It may be regarded as a compensatory reaction with respect to conspicuous visible movement, when that movement is due to the reacting insect's own locomotion, the attracting object remaining still (cp p 228) According to all the authors who have described visual attraction of hoppers to inanimate objects, the attraction is not evident when locusts are migrating steadily It is evident, in both hoppers and adults, only when they are ceasing migration or for the time being non-migrant This distinction between the behaviour of full migrants on the one hand and slackening migrants or non-migrants on the other was confirmed during the present studies (p 199)

The general impression that migrant swarms select for roosting the most conspicuous trees in the neighbourhood was also confirmed during the present studies (p 199) Lépiney mentions this phenomenon, and quotes cases where it was clear the attraction could not have been other than visual (cp Kennedy 1939, pp 447–9)

There was little evidence that swarms in full flight were attracted in the same way to conspicuous objects On the contrary, they avoided them as discussed in the previous section There is a popular belief among agriculturalists that swarms do descend for choice upon green (and in desert countries often therefore conspicuous) crops, but this may be a biased view Systematic and unbiased data on this matter would probably be difficult to collect, but one aspect of it invites experimental study, the effect of external and internal conditions on the locusts' responsiveness to the conspicuous objects they meet on migration Speaking of hoppers, Volkonsky (1942) states

> 'Cette attraction visuelle se manifeste de plus en plus au fur et à mesure que la végetation se dessèche Elle disparait lorsque la végétation est détrempée par une pluie où lorsque l'etat hygrometrique de l'atmosphère est élèvé '

Volkonsky never published the evidence for this statement, but there are some indications that the excitability of adults, and their orientation to wind, may depend on their water relations (below, p 247), so that the possibility of their susceptibility to attraction by conspicuous objects being conditioned in the same way would be worth investigating

Moisture

A number of authors have given consideration in recent years to moisture as an influence on locust migration There is some fresh direct evidence of its effects and some evidence from correlative studies of routine reports, while experienced students like Rao and Strelnikov have given their strong impressions on the subject

Volkonsky (1939) found that caged swarms of Desert Locusts engaged in spontaneous mass flying only when the mean relative humidity during the preceding 24 hr had been 65% or below, and except for four out of the nineteen occasions only when it had been 59% or below The total relative humidity range covered by Volkonsky's observations was 52 to 75% He discussed temperatures also, but unfortunately he does not give any detailed figures, and does not indicate to what extent his observations warranted clear conclusions regarding the separate effects of humidity

Concerning the pre-conditioning effect of air and insect water content upon the behaviour of the insects, Volkonsky remarks in a later paper (1942) that the tendency for individual Desert Locusts released from cages to embark on sustained, uni-directional flight is favoured by desiccation He also states (in quotation above) that the apparently visual attraction of conspicuous vegetation for gregarious hoppers is most evident when the general vegetation is drying up, and disappears again with a fall of rain or rise in air humidity Strelnikov (1936) found that hoppers lost half their weight in a day's march and states that water was the main material lost He goes on to say that the loss of water first increases 'irritability' and then causes depression Rao (1942) also stresses low humidity as an 'irritating' factor leading to the evacuation of first the winter-spring and then the summer breeding areas of *Schistocerca* in India Again he offers no direct evidence, basing his opinion on the correlation between the onset of hot desiccating conditions and the emigration of the locusts Partly from circumstantial evidence and partly from observations on caged locusts from swarms, Rao believes that locusts which have been subjected to drought conditions are particularly susceptible to activation by the stimuli (including moisture) brought by, or even preceding, rain or dust storms

In the laboratory Kennedy (1937) found that *Locusta* of all stages were activated by a rise and inactivated by a fall of humidity, provided the exposure times were short If successive dry and moist exposure periods lasted many hours no difference in activity was apparent Locusts starved for some days in a low humidity, continued to show a preference for dry air when offered a choice, partly through the kinetic reaction just mentioned Key (1936), on the other hand, found that older *Locusta* hoppers reared very wet were activated by exposure to a dry atmosphere, while those reared very dry were activated by exposure to a wet atmosphere

The results of these laboratory experiments are confused and incomplete, but further support for Volkonsky's, Strelnikov's and Rao's views comes from an observation by Tauber, Drake & Decker (1945) They found that *Melanoplus bivittatus* fed on fresh, moist plants were quiet and not easily excited, whereas when fed on desiccated plants the insects were 'hyper-irritable', jumping and flying about at the slightest disturbance

The most striking illustration of both humidity responses and humidity-conditioning of other responses comes from the field observations of Bodenheimer (1944) on *Dociostaurus maroccanus* To some extent these observations were anticipated by those of Shotwell (1930) on *Melanoplus mexicanus* Observing that *Dociostaurus* adults seemed to be attracted from a distance to his experimental pans of moistened bait, Bodenheimer tried pouring a small quantity of water on the ground when numerous locusts were sitting about nearby At once locusts from up to 20 or more metres away, and in a narrow cone of directions down-wind of the moistened sand, took off, flew low toward and came down at it From other directions only insects immediately adjacent to the water came to it, farther away they remained quite immobile The responses were most marked during the heat of the day, and the attracted insects 'drank' avidly from the wet sand grains Afterwards they flew off, now across-wind

The same results were obtained in repeated trials On one occasion members of a swarm already in flight, across-wind, were observed, as soon as they arrived down-wind of moistened sand, to turn up-wind and fly in a definite stream across the main swarm direction, to the moisture The experiments established the existence in *Dociostaurus* of

(i) *a conditional, direct, hygro-kinesis* locusts resting in relatively hot, dry conditions were strongly stimulated into flight by an access of moist air, whereas in other conditions they were less affected,

(ii) *humidity-conditioning of wind orientation reactions* moisture in the wind not only stimulated sensitized locusts into flight, but also enhanced or evoked the (probably optical) reactions leading to up-wind orientation, which ceased when the locusts had drunk adequately

It is not clear whether the effect on wind reactions was direct, in the insect, or indirect, a result of making the insects descend to where such reactions would become stronger anyway, on the optomotor theory (figure 13, p 213) The second suggestion is the simpler of the two behaviourally, but there are precedents, among insects, for the first suggestion of wind-borne substances evoking wind orientation (Flügge 1934, Tinbergen 1935, Kalmus 1942)

Bodenheimer's observations were confined to small, local movements, but point (1) could be important for long-range movements also, and supports Rao's suggestion above (p 247) The only case in which the idea of humidity-conditioned wind orientation has been put forward on the basis of a large body of data concerns the movements of *Chortoicetes terminifera* in Australia, analyzed by Key (1942, pp 31–34, 61–62 and 75–77) Correlating the predominant monthly flight direction in each locality with wind directions and humidity gradients, in 1937–8, he found that swarms flew 'more or less' up-wind in 49 % of cases but 'more or less' up the humidity gradient in 74 % of cases, there were 661 cases in all 'More or less' here means anything up to 45° to left or right of the due direction Thus the locusts flew up the humidity gradient but with or across the wind in 25 % of the cases A similar marked predominance of up-humidity-gradient flights were found in 1936–7 and in 1938–9

How much meaning these consolidated average figures have is very doubtful, for they tell us nothing about the actual wind and humidity conditions experienced by any swarm No conclusions can be drawn from the data about the reactions of *Chortoicetes* until direct observations under known conditions are available But it is important meanwhile to consider Key's suggestions in this connexion in the light of Bodenheimer's work and the optomotor theory of the behaviour of wind This subject has engaged the attention of other writers on insect migration (Williams 1949, Waloff 1946) We cannot yet answer the questions at issue, but the lines of future work will depend very largely on what is now considered more and what less likely to be the correct solution

Key's (1942, p 76) argument was as follows

> 'the simplest assumption would be that swarms orient their flight according to the direction of the wind, but discriminate between "moist" winds and "dry" winds, flying with the latter and against the former Owing to the marked tendency for moving air masses to retain the properties they possessed at their source of origin, down-gradient winds at any station are always moister than the mean relative humidity for the station, while up-gradient winds are always drier than the mean, and these departures may be considerable'

From what has been said here about wind orientation, and from Bodenheimer's work, it appears that Key may be proved right, as far as orientation against moist winds is concerned Given appropriately conditioned locusts, up-humidity gradient flights might be due to moist winds encouraging first taking-off and then up-wind orientation, whereas dry winds might discourage taking-off and be less likely to impose active up-wind orientation when flight does occur A moist wind might be able to induce up-wind orientation better than a dry wind for the further reason that the moist wind keeps the fliers low while the dry one does not, although Bodenheimer's evidence of this was not so good But there is no evidence to support Key's suggestion that dry winds produce down-wind orientation directly, that is simply by reversing the insects' reaction to moist wind

Williams (1949) has suggested that the humidity changes experienced by insects in the course of their local movements through the micro-climatic 'patchwork' and in the diurnal humidity cycle, are greater than those they would experience through changes in the wind direction The local changes would mask those due to wind changes so that the latter could have no clear influence on flight orientation The whole matter requires investigation, but this argument may not be as conclusive as it at first appears The laboratory experiments described and Bodenheimer's field observations, however explained, suggest that it is the *change* of ambient air humidity which is the effective stimulus for taking-off and enhanced orientation to wind The diurnal humidity cycle involves slow changes, and other factors like temperature and light confine the flights of locusts to a limited part of the diurnal humidity cycle More rapid changes will be experienced in moving through the micro-climatic 'patchwork', but it is also possible that the insects respond, not to humidity changes as such, but to them only when combined with wind

Key (1942, p 76) himself points out that 'flight up the humidity gradient might result from a differential response to winds differing in other qualities than moisture content, for example temperature or strength' There is reason to suppose the directing influence of wind (not *responses* to it) may be reversed by such other factors (see part II), but the possibility that humidity can similarly condition the wind's directing influence on some locusts, cannot be excluded

The effect of insect desiccation and wind moisture on wind orientation is not, however, conspicuous in the Desert Locust These conditions are by no means indispensable for up-wind orientation to dominate a whole migration trend, as witness the up-wind migration of the Desert Locust in early spring (p 203) when there is plenty of fresh green food available and the rains may still be on

Rain has often been described as having at least a temporarily hindering effect on flight and sometimes a spectacular one (Cheesman, 1929, Gunn *et al* 1948, p 52, Harrison, 1929, U S A 1878, 1880), but the effect of the accompanying drop in air temperature cannot be separated in the field from the effects of rain itself On the whole it appears that rain itself provides surprisingly little hindrance to migration, as appeared during the present observations (p 178) From her analysis of records of swarms found flying and settled at different seasons and in different districts in East Africa, Waloff (1946*a*) concluded that most of the reduction of flight activity occurring during rainy seasons was due to reproductive behaviour

Migration as a special type of behaviour

Only some of the aspects of the behaviour of migrant, adult, gregarious phase Desert Locusts have been discussed here, and deficiencies in our knowledge have been pointed out many times But we have now a sufficiently full picture of their behaviour, provided it is taken together with that of migrant hoppers, to deduce what essentially distinguishes migratory from other kinds of behaviour

Activity

The most unmistakable feature of the behaviour of *gregaria* locusts is their extraordinarily persistent locomotory activity Over a wide range of external conditions, swarms take to flight in the morning and fly on, or alight only to take off again repeatedly, until evening. And they do this day after day, once recovered from the last moult, and with some reduction during mating and egg-laying, until death The hopper bands behave in much the same way.

This 'irrepressible' locomotory activity naturally requires suitable environmental conditions, but these are conditions that can only be regarded as moderate and favourable for the species (pp 232–236) Conditions that are excessive or unfavourable to the species, such as extremes of heat and cold, strong wind, etc , restrict rather than enforce marching and flight External conditions thereby determine during which hours of the day or night, migration occurs in a given region and season (pp 233–234), but they do not 'force' it to occur Even the external influence of other band or swarm members is not essential for the *gregaria* individual to show its extraordinary activity (p 194) That influence seems to be an important means of reinforcing activity in bands and swarms (pp 224–225) but even so cannot be regarded as an extraneous force The *gregaria* individual is so constituted as to expose itself preferentially to its fellows' influence and is peculiarly sensitive to it We might regard as forced the development of the migratory habit during the change from the *solitaria* to the *gregaria* phase, since exceptional circumstances are required to bring this change about Once greganization is complete and we are dealing with locusts of the gregarious phase, however, sustained locomotion does not depend on circumstances that are exceptional in any way

If the behaviour of the solitary phase, or of most animals for that matter, be taken as a standard, then gregarious locusts are clearly abnormal in embarking on a course of sustained locomotion when conditions are in no way extreme But the fact is that such behaviour is normal for gregarious locusts (p 226) Under favourable conditions the solitary (or non-migrating *gregaria*) locust makes only intermittent movement through the day, periods of movement falling between longer periods of feeding, basking, mating, etc Under the same conditions, the migrant keeps up extraordinarily persistent movement, 'sedentary' types of behaviour, such as feeding and basking, becoming restricted in consequence to early morning and evening This migratory activity is characteristic of the insects themselves

> 'Flying with them (gregarious locusts) may be regarded as a normal state and rest is enforced by environmental conditions' (Uvarov 1947)

Persistent locomotory activity is not in itself what distinguishes the migrant, however Such activity is the normal behaviour of insects which are obviously not migrant, like whirligig beetles (Gyrinidae) or the many kinds of insects which form persistent swarms during the nuptial flight, such as mayflies (Ephemeroptera) What separates the behaviour of these insects from that of a migrant is not only the fact that they remain in roughly the same place, but also that their simple locomotion is readily interrupted by other kinds of behaviour feeding and mating, respectively, in the examples mentioned Indeed, the immediate effect of their locomotory activity is to expose them more effectively to the specific stimuli which interrupt it the whirligig beetle to floating food particles and the mayfly to its potential mates Their locomotory activity may be regarded as an essential part of the activities of feeding and mating The situation is reversed for the migrating locust Its behaviour is dominated by locomotory activity for hours at a time, day after day, to the virtual exclusion of all else Whatever ultimate effect this may have on the biology of the species it certainly has no immediate connexion with biological functions like feeding and reproduction

If this most characteristic feature of migrant behaviour is to be put into a phrase, it may be said that the *gregaria* locust is subject to a powerful 'locomotory drive' The term 'locomotory drive' is used here descriptively and objectively, implying neither consciousness nor directiveness It means simply that the insect is in a neuro-physiological state of a peculiar kind, such that its whole behaviour is subordinated to locomotion and other forms of activity are largely shut off

Direction

The observed tendency to keep a straight course The second characteristic feature of the locust migrant's behaviour is its tendency to move steadily in one direction This tendency requires careful definition, as the centre of much controversy Williams (1949, p 73), speaking of butterflies, has described the situation in this way

> 'During a migratory flight the path of each butterfly—which would normally have been here and there, backwards and forwards, leaving the insect at the end of the day more or less where it started—is straightened out so that the insect flies steadily in one direction '

Now it appears that steady flight in one direction occurs more often among butterflies than among locusts (Part II) And the tendency to fly straight may be less strong even in butterflies than Williams suggests, for it is difficult to see how he could be sure that one '"compass" direction can be kept up hour by hour and day by day by a single insect' (1949, p 73) At any rate, there is no evidence that locusts ever fly as straight as that and numerous cases are on record of direction changes under immediate observation by both hopper bands and adult swarms When single swarms have been followed day after day, the line joining successive night-roosting sites has proved to be a zigzag, not a straight line (Gunn *et al* 1948) And Waloff's (1946, p. 48, table I) analysis of the collected routine reports of Desert Locust swarms in eastern Kenya showed that the proportion of *all* swarms found in flight was almost always higher than the proportion of *flying* swarms found moving toward any one of the eight main sectors of the compass Flight itself, not flight in one direction, is the main characteristic of migrants

We are not here concerned, however, with the pattern of movements among whole populations of swarms, nor with the resultant direction of long-range movements the route of which can only be inferred, such matters form a separate study (Part II) We are concerned here with the movements of individual migrants, bands or swarms as directly observed and therefore over short distances and on or near the ground,

Among these, the direction of movement shows a fixity which, although very far from absolute, is striking by comparison with the more erratic movements of non-migrant locusts or other insects When the adult gregarious locust engages in the peculiarly persistent movement characteristic of the migrant, instead of merely making periodic short flights reaction to shifts of the retinal images of gross features of the landscape in the forward field of view. Other directing agencies have been suggested but not demonstrated, such as orientation reactions of the basking type, to radiant heat, which may be of some importance, particularly when migration starts.

These are all reactions to gross environmental stimuli, obvious to man. Reactions to stimuli less obvious to man, such as aerodynamic changes (p. 207), although perhaps mainly concerned in maintaining the insects' immediate stability in flight, should also be mentioned. They will help, if in a minor capacity, to promote straightforward flight.

These reactions are not peculiar to the behaviour of migrants. The mutual compensation reactions of gregarious locusts occur also when they are not migrating. Wind orientation, the light-compass reaction and movement toward the 'open', have not yet been demonstrated independently in non-migrant locusts, but have been demonstrated in other non-migrant animals (Fraenkel & Gunn 1940). There is no reason to suppose any of the reactions of migrating locusts are, as reactions, peculiar to their behaviour while migrating. The migrant differs from the non-migrant, therefore, in the changed *pattern* of its reactions rather than in any novelty about the reactions themselves.

The problem, then, is not to discover 'the methods by which migrating insects ... keep to a fixed direction over long distances and over long periods of time' (Williams 1942, p. 226). Nor is it, primarily, to discover some new kind of reaction. The problem is to discover how the several known reactions of the migrant to external features become *organized* into a particular pattern: a pattern which includes many changes of direction, but also a good deal of steady flying in one direction.

The organization of orientation reactions into the pattern peculiar to migrants. The point of departure in considering this problem is that similar reactions to the same external stimuli can produce, either direction changes, or straightforward movement, according to the circumstances. Changes of direction and straightforward movement have been set against one another in the past (see the quotations from Williams 1949, pp. 74–75, given on p. 252–3), as evidence of two distinct principles of orientation, temporary reactions to merely disruptive external features, and the special directional sense. If we dispense with the second principle, then field observations of changes of direction provide the natural experiments needed to elucidate the causes of unchanging direction. The next task, therefore, is to compare the circumstances under which these two types of movement appear.

Changes of wind speed or direction, when the wind is strong and the insects are flying low, provoke various reactions including changes of orientation. In a more moderate wind of fairly steady direction, on the other hand, low-fliers fly steadily on in one direction, say against the wind. According to the optomotor theory, they are kept on that course partly because any turn produces gross transverse image-movement which is compensated by a turn back into the up-wind orientation. Thus the insect itself, if it does not fly straight when there is a steady wind, produces gross changes in the apparent movement of its visible background. These changes brought about by the insect itself in a steady wind are comparable with the changes experienced by a steady insect subjected to a changing wind. In compensating the resultant image-movement, the insect minimizes the changes, and so flies straight ahead when the wind is steady but deviates when the wind changes.

When two columns of migrating hoppers or adults meet at an angle, compensatory responses of insect to insect cause mass changes of direction, or 'gregarious re-alinement', as when two bands or swarms cross, or when the wind induces 'gregarious reversal' In a single advancing band or swarm, not subject to the mass impact of insects moving in another direction, similar responses help to maintain steady movement in one direction (p 228)

A striking new feature in the landscape such as a tree or a glittering body of water lying across the path of migrant hoppers or adults, may cause them to change direction before actually reaching it But if such conspicuous features are elongated, like a shore-line or an avenue through vegetation, the movement of the migrants may be canalized along a path parallel with the line, straight or meandering, of the external features, the only path on which gross transverse image-movements can be avoided (p 245)

The sun-compass reaction is the one reaction to gross external features which is observed to cause only steady movement in one direction for considerable periods, and not changes of direction, under natural conditions Presumably the reason for this is that the sun's own direction, unlike that of the other features mentioned, does not change rapidly But if its apparent position be changed rapidly with a mirror, it does produce changes of direction, very strikingly (Kennedy 1945) In nature, it seems, it is only the insect's own deviations from a straight course which cause sufficiently rapid changes of the sun's position in the insect's eye to bring the sun-compass reaction into play, which reaction therefore serves to keep the insect on a straight course

Thus the evidence suggests a very simple conclusion the circumstances in which a change of direction occurs are those in which a gross change occurs in one or more of the external features to which the migrants show orientation reactions, while the circumstances in which movement is straightforward are those in which no such gross external changes occur Thus changes of direction, and fixity of direction, contrasted though they seem, stem from one and the same tendency on the part of the migrants That is the tendency to avoid, or rather minimize, changes in their sensory relations with the environment If these relations are sufficiently changed by a change in the environment, the migrants are caused to change their direction accordingly If the environment remains constant, then the migrants keep their own direction constant, for otherwise, if they deviate, their sensory relations with environmental features are changed as much as in the former case when those features themselves changed

The tendency to go straight as an outcome of the locomotory 'drive' In reacting to changes in the sensed environment in such a way as to minimize those changes, i e in a *regulatory* manner, migrants behave as non-migrants do Such sensory regulation is one of the most fundamental functions of behaviour in general and is no more peculiar to migrants than are the kinds of reaction by which the regulation is effected

At the same time, behaviour does not consist merely in maintaining as constant an environment as possible Behaviour consists of various positive activities by which the animal lives and reproduces itself, and it is these activities which are facilitated and guided, to some extent, by sensory regulation In the course of such an activity the animal undergoes major changes in its sensory relations with the environment, changes which it does not minimize by regulatory reactions, but which on the contrary it accepts and reacts to in ways that further change its external relations We may therefore make a working distinction between reactions having the immediate sensory-regulating effect of minimizing changes in the animal's environmental relations, and the function of smoothing the animal's path in the carrying out of a number of vital activities, on the one hand, and, on the other hand, reactions having the immediate effect of changing the animal's environmental relations, and the function of contributing directly to the carrying out of some specific vital activity, such as feeding or mating No teleological assumptions are involved here, even if, with the 'objectivistic' behaviour school (Tinbergen 1942), we designate the tendency to behave in a certain complex of ways associated with a given vital function, as a 'mood' or 'drive' named after the function (but see p 258)

The behaviour of the migrant is dominated by a locomotory 'drive', as we have seen Neither the kinds of orientation reaction, nor their joint, sensory-regulating function, are peculiar to the migrant, but the locomotory drive is In the migrant, locomotion becomes elevated to the status of a 'vital activity' It is in the locomotory drive, therefore, that we must look for the origin of the tendency to go straight, since that also is peculiar to the migrant For analytical purposes we may distinguish, quite artificially, two ways in which the locomotory drive transforms the pattern of regulatory reactions into one which results in straightforward movement

Consider first the external circumstances of the insect Compare the circumstances of a non-migrant locust, such as one of phase *solitaria*, or *gregaria* but non-migrant because engaged in reproductive activity, with those of a migrant *gregaria* locust Owing to the variety of activities on which the non-migrant spends its time—feeding, basking, moulting, mating, avoiding enemies, etc —it carries out only a limited amount of locomotion, and that intermittently It spends its time on the ground or vegetation where a great variety of conditions are found within a small compass It responds to the stimuli provided by many individual details of the habitat Each plant, for example, plays its individual part in evoking diverse responses, as a source of food, as shelter from wind, as shade from the sun, mechanically as a resting place, and as an attractant, conspicuous object Micro-climatically, the environment is a 'patch-work' Temperature, for example, varies abruptly from point to point, and the insect's thermokinetic responses seem to play a dominant part in its whole diurnal behaviour pattern The locusts' responses to such stimuli are seldom directed, and when they are, the directions taken are inconsistent While a shrub, for example, may serve as a directing (attractant) stimulus for a while, the insect soon reaches it and the shrub then resolves itself into a variety of other stimuli mechanical, thermal, gustatory, etc

The non-migrant's regulatory reactions help to keep it within its particular habitat, and therefore within a more limited range of conditions than it would experience without them But its movements within the habitat are in many directions and cannot possibly be in only one, when it is merely 'pottering about', responding to many incidental details of its environment in the course of a variety of 'sedentary' activities

Contrast with this the behaviour of the migrant For the migrant there is only one drive and one activity, not 'sedentary', but locomotory Impelled by its overriding locomotory drive, the adult spends its time in the relatively uniform environment of the air, out of reach of the kaleidoscopic micro-changes it would suffer on the ground The migrant hopper, too, keeps to the most open, uniform terrain accessible to it The four types of reaction suggested above as important in adult migratory behaviour are all *visual*. Compared with changes in the flying insect's field of view, other external changes, as of temperature and humidity, are slow and infrequent And while the non-migrant reacts visually to the individual shrubs about it as isolated objects, they become for the migrant merely units in a moving procession, and it is to this movement and not to the separate units composing it that the migrant reacts, on the optomotor theory, in orienting to the wind A single object must be large, striking and in the immediate line of flight before it can evoke a separate response from the migrant

Because the migrant is constantly moving on, it necessarily experiences continuous change at least in its visible environment, unless it is flying very high or in the dark It accepts these continuous small changes as a concomitant of its own movement, as a moving but non-migrant does in a more limited way, without reacting to each passing detail Because of the special environment it creates for itself, the migrant does not encounter sudden discontinuous changes as often, in a given distance travelled, as the moving non-migrant, but when the migrant does experience such changes in the environmental procession past it, it does respond, by regulatory reactions The discontinuities may be due either to the 'looming up' of outstanding new features as it moves along, or to a change in its relation to old, in themselves relatively unchanging, features like the sun, the wind or fellow-locusts, a change caused by its own deviation from a straight path As a result of regulatory responses to changes of this second type, the insect's deviations are minimized and the tendency to go straight emerges Thus the tendency to go straight is to some extent an indirect outcome of the locomotory drive, that is, an outcome of the peculiar external circumstances the migrant experiences The tendency is seen also in non-migrants, but is not so conspicuous there, partly because non-migrants do not travel so far in one movement, and do not remain in so uniform an environment

However, persistent locomotion does not necessarily create a tendency to go straight, even if it does so in gregarious locusts In some insects, such as the Gyrinid beetles and mayflies already cited (p 250), persistent locomotion is accompanied by frequent direction changes Despite their disorderly superficial appearance it is precisely through these frequent direction changes that continuously moving but non-migrant insects maintain an orderly, regulated relationship with their surroundings, either with some one conspicuous feature, as in midges (Gibson, 1945) or mosquitoes (Bates, 1949), or with several features in combination, as in Gyrinids (Brown & Hatch, 1929) The environmental relations of continuously moving insects may thus be stabilized in one of two types of orientation (i) by keeping a straight course through compensatory responses to those gross external features which remain with the insect, so to say, as it moves, while 'ignoring' incidental, local features, or (ii) by constantly changing direction through compensatory responses to fixed local features The latter appears to be a higher form of orientation, allied to what Tinbergen (1942) has called 'pharotaxis'

The difference between these two types of orientation evidently reflects a difference in the reactivity of the insects to similar stimuli, and in the pattern on which their reactions are organized internally Associated with those differences, the biological functions of the two types of orientation are also different The locomotion of non-migrants forms part of their immediate feeding or mating activities, while that of the locust migrant does not, having an uncertain biological effect which is discussed elsewhere (Kennedy, in preparation)

Moreover, if migrants travel farther, without being distracted by incidental features along their route, than do non-migrants, it is their locomotory drive which not only impels the migrants but which also prevents them reacting to the incidental features This is evident from the fact that when migration is slackening, but before the locomotion itself has ceased, the migrants change their reaction to conspicuous external objects, from avoidance of them to attraction to them (pp 199 and 245) We must picture the steady locomotion as the clearest expression of a generalized 'drive' or 'mood' (Tinbergen 1942) which expresses itself also in the detailed reactions of the insect—or, as we might say, in the insect's changed 'attitude' to the same external features That is not to say that the change of 'attitude' is determined wholly physiologically, by internal causes, and still less that it implies a conscious state It is probably the combination of the peculiar neuro-physiological state of the *gregaria* migrant, plus the peculiar pattern of its sensory experiences during continuous locomotion, which together bring about the change of 'attitude' during actual migration

In the whole complex of the *gregaria* locusts' migratory behaviour we have an example of instinctive behaviour in the broad sense of Lorenz's recently proposed usage that is (Tinbergen 1942, Thorpe 1948), behaviour comprising two main components There is a stereotyped automatism, either walking, hopping or flight, which is the instinctive action in the strict sense (*Erbkoordination* of Lorenz), and there is an elaborate, non-stereotyped 'coating' of reactions to specific stimuli (the '*Taxis*' *component* of Lorenz) which guide the automatism in operation

> 'The "Erbkoordination" can as a rule be released by a combination of external and internal factors Usually, the internal factors evoke a preparedness to react to certain external stimuli in a certain way, in other words, the external stimuli are more specific than the internal causes' (Tinbergen 1942)

Thus, the locomotory automatism appears in locust migration, as we have seen, mainly from internal causes of a general ('metabolic') nature, although it probably has to be released by trigger stimuli But, in addition, the same internal causes create in the migrant a special type of reactivity to certain external stimuli, the ones which the migrant experiences repeatedly as a result of its own activity

It is necessary, however, to bear in mind that we are dealing here only with behavioural events and not with physiological or psychological ones The observed behavioural events, such as persistent locomotion, or a particular pattern of regulatory reactions, are the effects of as yet largely unknown physiological causes to which the locomotory *drive* and sensory-stabilizing *tendency* are ultimately referable While it may be convenient to label such behavioural tendencies according to their specific effects or functions, this does not mean there is a comparable specificity in their physiological causes A merely quantitative physiological change, as in the concentration of a hormone or in the pattern of central nervous excitation, can produce a completely new pattern of behaviour Lorenz's concept of *reaction specific energy* seems unfortunate because it implies a specific one-to-one relationship between internal cause and external effect If we visualize a given behaviour pattern as caused by some equally specific, counterpart material, 'energy' or process in the nervous system, then it is all too easy to translate this directly into subjective terms If the behaviour pattern be conceived as existing in some potential, already-differentiated form in the animal before it appears in overt acts, then cause and effect become reversed, and we have something very like a pre-existing idea or purpose postulated as the cause of the overt act

When speaking of the locust's locomotory drive, therefore, we mean a behavioural tendency having definite physiological causes which have yet to be discovered, and not a tendency attributable to a subjective urge or 'appetite' for locomotion (cp *preference*, p 212) At the same time, while we are dealing with behaviour we can recognize the locomotory drive, and the sensory-stabilizing tendency, as tangible and important entities, the effects of which can be examined although we do not yet know their physiological basis

Locomotion is a relatively simple activity from a behavioural, if not from a physiological, point of view It does not involve the elaborate sequences of different reactions to specific stimuli, such as are involved in the other kinds of instinctive activity that have been cited in this discussion feeding and mating During the latter activities, these specific reactions prevent the animal from stabilizing its environmental relations to any striking degree, although immediately regulatory reactions are also occurring frequently and serving to minimize external changes which would otherwise disrupt the given specific activity The behaviour of the migrant, however, is made up, apart from its locomotion, almost entirely of reactions of the immediately regulatory type This is, no doubt, one reason why migratory behaviour has often seemed to be something quite apart from all other kinds of behaviour The migrant's tendency to go straight is the sensory-regulating type of behaviour maintained in so exceptionally pure a form that it has given the impression of veritable independence of the environment, instead of the delicately adjusted, direct dependence which it in fact expresses

The tendency to go straight, and the going itself, are both outcomes of the locomotory drive That drive, the only feature peculiar to or 'innate' in migrants, is not itself directional in any sense There is no '*directional* urge' in the migrant, no 'innate sense of direction' Locomotory activity—'going'—is more persistent and unconditional than going straight It is the direct outcome of the causes subsumed under the term locomotory drive In that sense locomotory activity is the primary aspect of migratory behaviour, while going straight is a secondary one Going straight is more conditional, an outcome not only of the special locomotory drive but equally also of the general function of sensory regulation Going straight is simply a means of solving an old biological problem in a new context the problem of environmental stabilization in the context of persistent locomotion

Locomotory 'drive' versus sensory regulation the key to migratory behaviour The external changes to which an animal makes regulatory responses are commonly changes to which it exposes itself, in the course of its activity under the influence of one or other type of 'drive' Nowhere is this seen more clearly than in the behaviour of migrants Migrants 'keep their environment as constant as is compatible with their own continued movement' (Kennedy 1945) In this connexion orientation reactions have received a disproportionate amount of attention, for they are by no means the only ones employed by migrants in regulating the changes they bring upon themselves They vary their height of flight, and even the amount of their locomotory activity itself, as part of their regulatory reactions Sensory regulation of many kinds is constantly brought into operation by the insect's locomotory activity

The migrating insect's two inseparable tendencies, the tendency to *travel* with consequent exposure to sensory changes, and the tendency to *minimize* those *changes*, are best illustrated from the behaviour of adult locusts in wind The wind is very liable to sudden changes, and since it bears the locusts, it is the most disruptive influence with which they have to deal The locust's regulatory reactions to the stimuli provided by the wind tend, if they seldom entirely manage, to keep the locust's displacement over the ground under its own control, that is, to keep its ground speed close to its air speed and its track close to its course On the optomotor theory, that is a consequence of the locust having a certain preferred retinal velocity and air speed The reactions evoked when the wind causes departures from these preferred values have the effect of minimizing the wind's tendency to deviate tracks from courses and indefinitely to raise ground speeds High ground speeds, due to down-wind flight, are compatible with maintenance of the preferred retinal velocity and air speed, at moderate height But in practice, the increase of wind speed with height favours lower, up-wind flights (p 223), and the variability of wind speeds militates against the perpetuation of a given course higher up where intermittent settling is not a ready means of sensory regulation The locust can keep control, in the objective, resultant sense indicated, without regulating its behaviour according to the wind so long as the wind speed is well below the locust's own air speed But when the wind is stronger, the locust's regulatory reactions come into play and help it to keep control, but cannot completely succeed because the wind is so erratic a force

Thus, were the regulatory tendency clearly shown by the locust's reactions to be taken, hypothetically, to its logical conclusion, so as to give the insect complete control over its ground speed and course, it would fly only when the wind was negligibly weak But its locomotory drive will not allow that, and it does fly in wind The regulatory tendency shows itself in the insect's settling repeatedly, if near the ground, whenever the wind begins to carry it backwards Again, were the evident regulatory tendency taken to its logical conclusion, the locust would always fly near enough to the ground to be able to see its wind-created, apparent movement and minimize it, by orienting against the wind and settling when no headway could be made But its locomotory drive, its tendency to climb in certain circumstances and the thermal up-currents to which it exposes itself, prevent it from staying within quick-settling range of the ground, or even within visually responsive range of it If it sees it is being carried away but cannot quickly settle, it turns down-wind where at least it is going the same way as it is facing, the only form of control left to it And its own activity often leads directly or indirectly to its losing even that amount of control

The locust migrant is engaged, in effect, in a constant struggle against the sensory disruption engendered by its own irrepressible locomotion The key to its whole behaviour is the opposition between two powerful tendencies combined in the same insect the tendency to locomotion and the tendency to sensory regulation

PART II A THEORY OF LONG-RANGE MIGRATIONS

SUMMARY

Cartographical analysis of the seasonal and geographical patterns of Desert Locust migration points unmistakably to wind as a key element in the determination of long-range migrations Cartographical and behavioural analyses show that the consistency of direction responsible for long-range trends is not created in the same way as the striking stability and unanimity of direction immediately observable during flights over short distances, which was considered in Part I Long-range movements are resultant trends, emerging from a mesh of more or less confused movements Behaviour analysis indicated that there was a constant struggle between the locusts and the wind for control over the locusts' displacement over the ground Displacement through the forward flight exertions of the locusts and displacement through being carried by the wind are both common and can continue for long periods It is obvious that wind-dominated displacement could create a long-range trend, and the behaviour observations indicated that locust-dominated displacement too could create a trend, but again, only under the influence of the wind The following theory of long-range migration is, therefore, put forward

The creation of geographically directional trends Displacement due to the locusts' own exertions can develop into a geographical trend if the locusts persistently resist carriage on the wind and make headway against it, actively orienting into it at least intermittently Displacement due to wind carriage can develop into a trend if the locusts persistently fly, yet signally fail to resist carriage on the wind and go with it There seems to be no other basis of long-range trend-creation Locust-controlled and wind-controlled displacement thus tend to be in opposite directions, up- and down-wind respectively An actual geographical trend appears among the swarms in a given region and season when one of the two kinds of displacement predominates decisively over the other

External and internal factors can help or hinder the locusts' resistance to wind carriage An important means by which external factors do this is by influencing the height at which the locusts fly, for the higher they fly the less they can resist wind carriage These helping and hindering factors act in a valve-like manner and are therefore called 'rectifiers' They do not cause displacement, nor direct it, but they do determine how fast and in which out of various possible directions a trend will actually occur They determine whether the locusts or the wind shall mainly effect the locusts' displacement and so determine whether the over-all displacement shall be up-wind, down-wind or negligible The outstanding rectifiers seem to be temperature, locust age and the wind itself Steady and moderate winds, moderate temperatures and the vigour of fully hardened locusts favour up-wind displacement Gusty and stronger winds, high temperatures, active convection and the weakness of young locusts favour down-wind displacement Geographical trends tend to, but do not always parallel the *prevailing* wind direction, for the most frequent wind may not be the one having the strongest rectifying qualities

Organization of trends into a pattern The pattern of trends reflects the swaying fortunes of locusts and wind as rival agents of locust displacement The pattern of rectifiers moulds the pattern of trends When a new generation of swarms is appearing at the start of a new dry season, the high temperature and weakness of the locusts conspire to minimize the locusts' control over their own displacement, rectify their displacement down-wind and produce a spectacular geographical shift of the whole population of swarms Such seasons alternate with seasons of more confused swarm movements, in which lower temperatures and the fully developed powers of the locusts combine to put them on a more equal footing in the struggle with the wind Control passes now to the locusts, when up-wind trends may appear, and now to the wind, when down-wind trends appear Often, the two are so evenly matched as agents of displacement that there is no predominant trend one way or another The cartographical confusion among swarm movements in the in-between seasons is due partly to the transition from one prevailing wind direction to another Geographical redistribution of the swarm population is due in these seasons, more than in the others, to regional temperature differences acting, to use an analogy, ortho- and klinokinetically In other words, swarms disperse in and from warmer regions where they fly more, and more straightforwardly, and become trapped in cooler (often mountainous) regions where they fly less and change direction more

Make-up of the whole pattern Multiplication and mortality are essential elements in the whole pattern of migrations They determine where swarms will be available to start on migrations, and where migrations must end for lack of migrants The environmental patterns (rainfall and temperature especially) mould the migration pattern, therefore, not only behaviourally and mechanically, but also in these 'biological' ways Some trends are regularly 'abortive' in the sense that they do not lead to new breeding grounds, while other trends are regularly 'successful' in that they do lead to new breeding grounds Many successful and spectacular long-range movements are made when the insects have *least* control over their own displacement The whole pattern involves the cyclical repetition of both abortive and successful trends

When tested in a preliminary way against known examples of long-range migrations, this theory shows promise, but its validity cannot be properly gauged until much more information of a suitable type has been amassed

Other ideas of insect migration are discussed in relation to the present theory, such as that long-range directional movements cannot be explained in objective terms and imply the existence of an innate sense of direction, that such movements are essentially passive, that no explanatory hypothesis can be expected until the complicated interaction of the many factors involved has been unravelled, and that migrants are guided by some one physical agency yet to be discovered It is emphasized that, in essence, long-range migration trends are not behavioural but rather ecological events

INTRODUCTION

The previous part attempted a causal analysis of Desert Locust migration considered as a type of behaviour The present one attempts a causal analysis of the geographical pattern of migrations, and, in particular, of the more spectacular long-range movements which form a part of that pattern It is usual to treat these two problems as one, rather than separate them as is done here But, for reasons that will be given, we cannot assume that the direction of migration over short distances, as observed directly, is determined in the same way as the direction of migration over long distances, as inferred from maps on which reports from all sources are plotted In studying migration patterns we have to deal, not with the behaviour of a sample of migrants in the particular circumstances under which close observation has been possible, but with the net geographical displacements of whole populations of locusts a problem of a different order The present analysis starts, therefore, from the evidence on migration patterns derived from synoptic studies of routine swarm reports The relevant behavioural information is then drawn upon for the construction of a new theory of the causes of long-range migration trends

THE EVIDENCE FROM CARTOGRAPHICAL ANALYSIS

The large-scale patterns of locusts' migrations are probably better known than those of any other insects There are fewer scientifically interested field observers of locusts than of, say, butterflies, but there is an army of economically interested locust observers whose reports have been collected for years The first detailed study of such reports concerning the Desert Locust was Predtechensky's (1935*a*), on migrations in Persia and adjacent countries The pre-requisites for more fully documented studies had already been provided in 1929, when the Anti-Locust Research Centre was established in London, and in 1930, when the International Locust Conference at Rome agreed that reporting arrangements be improved and all reports sent to that Centre for collation The accumulated material was first presented in the form of annual summaries of movements and breeding (Uvarov 1933*a*, 1933*b*, 1934, 1935, Uvarov & Milnthorpe 1937*a*, 1937*b*, 1939) Since then, the seasonal patterns of breeding and migration of the Desert Locust in single regions have been analyzed and published (Rao 1942, for India, Waloff 1946*a*, for eastern Africa, Donnelly 1947, for West Africa) The subject has passed entirely beyond the stage of ingenious inference from fragmentary data, which was all that was possible when Bodenheimer (1932) made his bold, speculative sketch of the cycle of Desert Locust swarm movements Information services are still imperfect and interpretaion of the information sometimes difficult, but it is now possible to draw conclusions on a firm foundation of facts, and even to give countries advance warning of locust incursions

The migration patterns that have emerged from all this work are not yet complete and present a complex and fluid appearance Reducing the movements to a system of distinct trends is not easy No two years show quite the same pattern, and yet several years must be taken into account in delineating trends with sufficient assurance These points are stressed because insect migrations are often thought to be more regular than they are The trends finally revealed in this way are real, nevertheless

Knowing the migration patterns, the next task is to establish their relation with the patterns of weather and geography With that aim in view, a great deal of statistical work has been done on the Australian Plague Locust (*Chortoicetes terminifera* Walk) (Davidson 1936, Key 1938, 1942, 1943) The value of undertaking the heavy task of such detailed correlations in ignorance of likely causal connexions seems rather doubtful, and Predtechensky (1935), Rao (1942) and Waloff (1946*a*) have confined themselves to drawing more general conclusions concerning the influence of the environment upon the Desert Locust's migrations Waloff's work in particular led to conclusions directly relevant to our problem of the behavioural basis of long-range migrations by the Desert Locust

Her general conclusions were as follows

The pattern of breeding areas and migrations is complex and inconstant Major trends represent merely predominant, not universal behaviour among the swarms concerned However,

> 'The seasonal trends of migrations and the changing location of breeding areas combine to produce a fairly regular pattern of seasonal distributions over East Africa This regularity depends on the physiological responses of the locust to climatic factors, whose pattern changes from season to season in a regular manner, and is not due to migration or breeding cycles inherent in the species '

It is clear from Waloff's work that although the locusts fly with extraordinary persistency, their movements do not suggest any search for suitable breeding areas, or for food (cf Uvarov 1928, 1944) Their movements are too disorderly to suggest a set tendency to fly in a particular direction They have no 'goal' Although the directions they take must therefore depend on external factors there is no one such factor with which locust movements are consistently related The direction of migration must be determined by a complex of causes and not by any single type of reaction or single external factor

The positive findings of Waloff's study were as follows

(1) Flight activity persists as long as the average monthly maximum temperature exceeds 20–22° C (cp Predtechensky 1935), a conclusion borne out by independent evidence on the air temperature at the time of departure of swarms in the morning (Gunn *et al* 1948)

(2) Swarms rapidly evacuate areas where the weather is hot and dry

(3) Flight activity is reduced during egg-laying periods in rainy seasons, but not noticeably by rain as such

(4) The main effect of physical relief appears to be in reality an effect of temperature on activity—swarms become trapped in the highlands in the cool season, and are then released and spread out from there when temperatures rise

(5) 'Apart from some important exceptions when swarms migrate across or against the wind, the major trends of migrations are down the prevailing winds, and change with them '

(6) 'The distribution of swarms at any season is thus largely dependent on the pattern of air temperatures and winds '

We are not directly concerned with *breeding* when trying to interpret migration patterns in behavioural terms Breeding areas represent temporary halting-places for sexually-mature swarms and the points of origin of immature ones In this way they form an essential element in the seasonal pattern What principally determines their location is fairly clear 'The incidence of breeding depends, among other factors, on the incidence of suitable rainfall conditions Because of this and of the mobility of swarms, the location of breeding areas is not constant, but follows seasonal changes in rainfall distribution' (Waloff 1946*a*)

Nor need another essential element in the seasonal pattern, variations in flight *activity*, detain us, except for its part in determining direction (below) Flight activity, dependent primarily on temperature, is restricted until 'fledging' is complete and is temporarily reduced during mating and egg-laying Other environmental factors, such as moisture in the air or the vegetation, atmospheric pressure and rain, do not seem to have an important effect on the amount of flying done by Desert Locust swarms, whatever may be their effects on other aspects of swarm behaviour, on other phases or other species

Our main problem is not breeding nor activity, but the *direction* of trends, the third essential element in pattern determination The results of cartographical studies point unmistakably to *wind* as the key factor underlying the direction of major movements In the first place, if we reject, as a mere label on our ignorance, the idea of a long-range directional 'sense' or 'instinct' within the insect, we must look for a long-range external agency We are not looking for an external agency which could make all swarms fly in the same direction during any season The records show very clearly that swarms do not move in that way We are looking for an external agency which can make enough of the swarms move in the same direction enough of the time to produce an overall trend of migration Wind is an external agency which seems able to fill this role More inflexible agencies, say the earth's magnetic field (Cockbill 1942) or its rotation (Chauvin 1947), the influence of which is purely hypothetical, can be neglected until the lack of any other explanation forces us to consider them The relation between winds and migration trends is too close to be coincidental There are significant exceptions, but the great seasonal trends are mainly with or against the prevailing wind, usually with it

THE BEHAVIOURAL BASIS FOR THE CREATION OF LONG-RANGE MIGRATION TRENDS

In full accord with the cartographical evidence, the direction of migrants as observed directly over short distances shows no constant relation with the wind direction Many authors have emphasized this, the latest to do so being Gunn *et al* (1948) Indeed, the importance attached to this finding seems rather excessive A constant relation between wind direction and locust direction could hardly be expected, considering that locusts have been seen flying in winds that ranged in speed from well below to well above the air speed at which the locusts themselves can fly Nor does the lack of a fixed relation between wind direction and locust direction mean that the locusts are indifferent to or independent of the wind On the contrary, it is the very variations in this relation which provide the best evidence that locusts respond actively to the wind The variations are not random, but regularly related to the wind speed and height of flight This has been discussed elsewhere, in part I, the provisional conclusions reached may be stated very briefly as follows

Desert Locusts orient themselves actively (probably by optical means) to the wind Near the ground they fly against the wind unless it is so strong that they can make no headway, whereupon they turn across and preferably down-wind, or settle At intermediate heights they are oriented only by winds too strong for the locusts to make headway into wind, and so tend to fly down-wind Higher still they are not oriented by the immediate wind, but inevitably their tracks are biased down-wind

Assuming that the wind has these effects upon the direction of migrants, the question at issue is whether the effects could create long-range directional movements Before this question can be answered we must consider to what extent long-range migrations really are directional As already stated, the mapping of swarm reports shows that movements are by no means directional in the sense of there being uniformity of flight direction among all the swarms involved in a given trend And single swarms have often been seen to change direction even within the short period they could be kept in sight by fixed observers Further information on this point has recently been provided by the unique observations of Gunn *et al* (1948), who were able to locate the roosting sites of two swarms for many successive nights The roost-to-roost directions changed from day to day, each complete track zigzagging and even sometimes doubling on itself In each case, nevertheless, a considerable *resultant* displacement of the swarm had occurred in a certain direction by the end of the period Flight at higher levels, or over the sea, or in gales, may result in very extensive movements in one direction But Rainey & Waloff (1948), who selected for study just such flights, produced good circumstantial evidence that even they occur in varied and changing directions in the same period and region It is rare to find a number of swarms moving in the same direction day after day (for examples of this, see pp 275–276) On all the available evidence, we must visualize most extensive swarm movements as made up of resultant displacements which emerge from a complex of variable movements and which, when sufficiently large and sufficiently alike among a number of swarms in the same season and region, add up to a long-range trend

Clearly, the consistency of direction seen in a long-range trend is a very different thing from the stability of direction so characteristic of migrants as seen at any one place Over short distances and periods (from seconds to minutes and even, on occasion, perhaps to hours) the direction of flight of migrants is strikingly constant The causes of this have been discussed elsewhere (Kennedy 1945 and part I) and are believed to include 'gregarious inertia', the sun-compass reaction and other behavioural consequences of the migrant's locomotory 'drive' But none of these direction-stabilizing agents appears to have any lasting action They are essentially stabilizers of the direction of the recent past, in whatever way that was determined Passing to consideration of flights over rather longer distances and periods (from minutes to days), the constancy of direction tends to disappear. And the wind, in particular, often impresses the observer as a main cause of the directional irregularities he finds, the very opposite of a direction-stabilizer Generally speaking, it is only when we consider flights over even longer distances and periods, and among a number of swarms, that directional consistency emerges again, in the resultant form described

Hence long-range migration trends are not simple extensions of short-range movements in a fixed direction, but represent a new, higher-order form of directional consistency If so, the possibility remains that long-range directional consistency is after all determined by the wind, although the wind is often the enemy of short-range directional stability

In the behaviour analysis (part I), attention was naturally concentrated on what the locust itself did when stimulated by air movements But the moving air does more than provoke reactions, it is at the same time the locusts' medium, it bears them Indeed, on the optomotor theory, it is because the wind bears them that it provides stimuli to which the locusts respond

The moving air is constantly tending to carry the locusts 'passively' over the ground, that is, independently of their flight exertions and orientation The resultant tendency of the locusts' whole behaviour, on the other hand, is to make that displacement (their *track*) reflect only the locusts' own exertions and orientation (*course*) *In short, there is a constant struggle between locust and wind for control over the locusts' displacement*

It has been pointed out (part I, p 259) that the key to the migrant's behaviour is its irrepressible locomotion The other peculiarities of its behaviour can be traced to its locomotory 'drive', being expressions of the well-known, sensory-stabilizing tendency of nervous reactions, now operative in the special context of constant locomotion In other words, the migrant's reactions tend to minimize the sensory disruption created by its own locomotion Seen in perspective, the struggle between locust and wind for control over the locust's displacement is merely one aspect of that essential contradiction between the migrant's two powerful tendencies, movement and sensory stabilization

The word 'control' is used in this connexion in a strictly objective sense A locust is defined as having control over its own displacement when, that displacement being apparent to it, it keeps its ground speed at or below its air speed and its track close to its course Keeping control in this sense is an outcome of the insect's preference for a certain retinal velocity and air speed, the locust keeps control (i) by energetic flight, (ii) by commonly flying low enough, and in sufficient light, for its speed and direction with reference to the ground to remain apparent to it, (iii) by orienting itself with reference to that apparent movement, and (iv) by descending and settling when the wind speed exceeds the insect's maximum air speed

So long as the locust is able to keep control in this way, its ground speed will be rather low (not exceeding its own airspeed) and *its track will have an up-wind tendency* The latter will not be more than a tendency, for locusts fly even when there is so little wind that the locusts' control over their displacement is virtually complete without their having to orient on the wind. But since they fly also in stronger winds, when control can be maintained only by active orientation, it may be said that flights under the locusts' control will have an up-wind bias And in the absence of an overriding bias in some other direction, the up-wind bias will create an over-all tendency to up-wind displacement among self-controlled fliers The strength of the tendency will increase with the strength of the wind

The situation will be quite different if the locusts lose control over their own displacement A locust is defined as having lost control over its own displacement when, that displacement being no longer apparent to it, it is unable to keep its ground speed below its air speed and its track close to its course Loss of control will impose a down-wind tendency on the locusts' tracks Again, this will be no more than a tendency, for locusts fly when the wind speed is much less than their air speed so that their tracks can be up- or across-wind, even if they are not actively controlling their own tracks because they are flying high, or in the dark, and cannot see the relative movement of the ground But locusts fly also in stronger winds, and it is obvious that the displacement of any air-borne insect not showing a sustained preference for up-wind orientation must develop a down-wind bias, if the wind speed and the insect's air speed are of the same order Furthermore, locusts exercising what may be termed partial control, that is, flying in winds too strong for them to make headway but high enough to maintain their preferred retinal velocity and air-speed by turning down-wind, will then move down-wind at the maximum possible ground speed for the given wind speed Thus loss of control creates a down-wind bias which will, in the absence of an overriding bias in some other direction, create a pronounced tendency to down-wind displacement Again, the strength of the tendency will increase with the strength of the wind

If locusts in control of their own displacement have a tendency to move up-wind, and those that have wholly or partially lost control have a tendency to move down-wind, we have here a possible basis for the creation of trends, and the crucial question then becomes what, in turn, determines the amount of control the locusts have over their own displacement?

The principle of 'rectification'

An example of a trend created, apparently, by externally imposed changes in the amount of control exercised by the insects over their own displacement, is provided by Beall's (1941, 1942) observations on Monarch butterflies (*Danaus plexippus* L) on the northern shore of Lake Ontario This case has several advantages as a first example of trend-creation The whole process was observed at one place, an exceptionally favourable circumstance not yet encountered with locusts (although very similar behaviour has been observed in locusts, see part I, p 192) Secondly, Beall's observations were made in the autumn when these butterflies are seen migrating southwards over a great part of the North American continent (Williams 1949 *et ante*) The specimens Beall watched moved southwards out over the lake whether the wind was blowing from north or south, which might be regarded as evidence of a directional urge driving the insects southwards regardless of the wind Yet the unusually full account Beall gives of what he saw permits of a different interpretation If so, his work deserves particular attention because the idea of a directional urge, derived from the study of butterflies, has been applied to other insects including locusts (Williams 1930, 1942)

Beall observed that with a wind from the north some butterflies flew northwards against it, keeping very low over land and water But at the same time a larger number at a greater height were drifted southwards over the water by the wind while still headed northwards With a wind from the south all insects seen flew southwards against it, keeping low over the land and water, higher fliers were not seen These observations show that the southward trend was not due to the butterflies being under an inner compulsion to fly that way The winds from north and south, so far from being merely incidental features of the situation, were actually responsible for the majority of migrants moving always in the same direction, southwards from shore to lake

This persistent off-shore trend falls into place alongside other observations on insects in wind, if we assume that the insects respond to the apparent movement of their visible substrate There is evidence for that assumption (Kennedy 1940, and Part I), and, if it be correct, the off-shore trend can be attributed to the fact that the 'maximum compensatory height' is greater over land than over water In other words, the relative movement of the ground due to the insects being carried over it by the wind remains sufficiently apparent to them to evoke orientation and height-varying responses, at a greater height over land with its profusion of large landmarks, than over water with its finer, more uniform, visible pattern

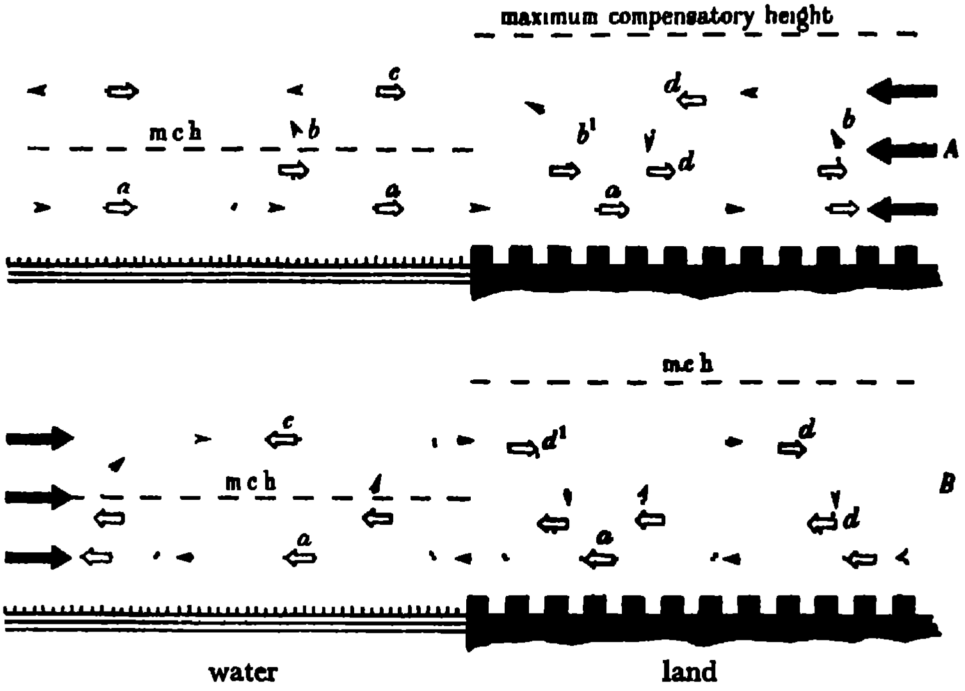

FIGURE 14 Diagram of the postulated 'rectifying' action of a land-water junction upon the movements of flying insects, based on the optomotor theory of behaviour in wind and the observations of Beall (1941, p 127) on *Danaus plexippus* L Resultant movement is from the land out over the water, both when the wind (heavy black arrows) is blowing off the land (*A*) and when it is blowing off the water (*B*) Outline arrows orientations of insects, dotted lines with simple arrow heads paths of insects Further explanation in text

The probable course of events is best described by reference to figure 14

When the wind is from the north (off-shore) (figure 14*A*) low-fliers will respond to it and so make halting progress up-wind, northward, over land and water (*aa*), rising in the air during calmer spells (*bb*) When the wind speed increases to above their air speed, fliers below the maximum compensatory height will soon turn down-wind and descend, to settle or to resume their slow up-wind progress in the weaker wind close to the ground (*dd*). The maximum compensatory height for any given wind speed is greater over land than over water. Many higher fliers that are hit by a wind gust while below the maximum compensatory height over land (b^1) will start the responses (descent, etc) which would ultimately arrest their down-wind displacement, but will find themselves over the water (c) before these responses have succeeded in arresting that displacement Over the water, the insects will now be above the maximum compensatory height, will cease to respond and will be carried farther and farther on the wind The opposite, up-wind, northerly movement is slow, being arrested and even reversed by every gust The resultant displacement will be southward, with and on the wind, because once over the water the insects' ability to resist carriage by the wind is drastically reduced

When the wind is from the south (on-shore) (figure 14*B*) low fliers (*aa*) will make halting progress up-wind over land and water as before As before there will be only a limited amount of carriage of higher fliers by the wind over land because the maximum compensatory height is great and the insects' responses to being carried down-wind soon arrest their down-wind displacement (*dd*) As before there will be relatively free carriage even of only moderately high-fliers over water (c) where the maximum compensatory height is small With-wind displacement will, however, be limited, for the simple reason that it will quickly take the insects over the land (d^1) where they can stop it The resultant displacement will be slow but southward, into the wind, because the wind's tendency to carry the insects with it is restricted, leaving the insects' contrary tendency to move up-wind predominant in effecting their displacement *

Thus the persistent off-shore trend arises because when the wind's direction reverses from on-shore to off-shore, its effect on the insects' resultant displacement also reverses A full interpretation of Beall's observations would require consideration of other points, such as the relative strength of northerly and southerly winds, the insects' probably unequal readiness to alight on land and water, the lack of wind-braking obstacles on water, and so on But these are ancillary points which do not affect the principle involved

The action of the land-water junction on the displacement of the insects may be likened to that of a valve, it encourages displacement in one direction but hinders it in the other There is no English verb-form of the word valve, to describe the action of the land-water junction, so it is proposed to borrow the term 'rectify' as a verb used in a similar sense in the terminology of electrical circuits † This particular rectifying effect has been observed in both butterflies and locusts, but can hardly be of first importance in creating the migration trends of either But, if there are other and commoner ways in which the locusts' control over their own diplacement is enhanced or weakened in a systematic manner, then the rectification principle may be of real importance as a means of long-range trend-creation

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* Dr W H Thorpe has pointed out to me that an on-shore wind would tend to accumulate resting insects along the shore, by this same action that causes flying insects to move out from rather than in toward the shore This action may help to build up the assemblies of Monarchs observed not only on the shores of the Great Lakes but also on the Southern California and Florida coasts

† No close parallel is meant with any of the numerous devices by which circuit elements are arranged to 'rectify' alternating currents The term is used here to designate a natural process of a type that is most difficult to cover with a single term A special term is necessary because this type of process, of which rectification is but a special case, is common and quite distinct, viz the establishment of an overall pattern from elements that are not *in themselves* responsible for it, but become so by virtue of their particular interrelationship Thus rectification is the process by which a behaviour pattern, in itself capable of producing movement in a variety of directions, is transformed into an essential causal element in the production of movement in one particular direction I am particularly indebted to Mr D R Newth for constructive criticisms here

'Rectifying' agencies

Locusts retain control by flying near the ground and settling when they cannot make headway against the wind If they persist in flying when they cannot make headway or fly too high to see they are being transported, they lose control, which passes to the wind It follows that *anything tending to restrict the amount and height of flight tends to keep courses and tracks up-wind and ground speeds low Anything tending to increase the amount and height of flight tends to make courses and tracks down-wind and ground speeds high* Agencies which affect the amount and height of flight (or the visibility of the substrate) thus become *rectifying factors*, theoretically capable of creating long-range directional trends of migration Such agencies are not difficult to find Evidence that the various environmental influences affect migrant locusts' behaviour in the ways to be described below, has been given in part I

Various aspects of the *wind* itself are manifestly rectifiers Take first those aspects which favour locust-controlled displacement, that is, movement against the prevailing wind They are wind speed generally low, seldom exceeding 5 m /sec , and wind direction steady, in other words settled weather without much interference from storms or strong winds Such were the conditions in south Iran in spring, 1943, when migration, both as observed directly and as deduced from the shift of swarm populations across the map, was against the wind and rather slow Winds were often negligible at the time of observation and the migrants were often flying well above the ground, probably beyond the maximum compensatory height But conditions of steady and weak winds are clearly also those giving the maximum opportunity for the stabilizing factors to maintain an orientation only intermittently imposed by the wind Under such conditions the orientation assumed at the morning departure from the roosting site would have a good change of survival for hours

It is suggested that the striking observation of de Lépiney's (1928) in Morocco comes within this category Both adults and hoppers migrated consistently to north-north-east for 6 days This might perhaps be explained as follows Both hoppers and adults first oriented perpendicularly to the rays of the morning sun while basking before migration started Some would of course be facing roughly south and others north at this time, but when migration began the balance was tipped in favour of the northward orientation by the wind blowing from the north-east (this sequence of events was observed in Kenya on 13 May 1944, part I, p 172) The locusts moved off north-north-east, their orientation maintained through wind lulls, temporary changes in wind direction and when the locusts were above the maximum compensatory height, by gregariousness and probably the light-compass reaction

Unless the wind direction be steady, as well as its strength moderate, up-wind migration may lead to a series of moves now in this direction and now in that, amounting to little or no geographical displacement over a period In a season of light winds of variable direction such up-wind flight as occurred would thus not bring about any major geographical displacement This may be one reason, among others, such as cold, reproductive behaviour, etc , for the confused periods between periods of major migration movements

Wind conditions which tend rather to deprive locusts partly or wholly of control over their own displacement, and so to favour with-wind movement, are of several kinds

First, when the wind continues very violent and gusty, locusts can be swept away with it (part I, p 183) Even if the locusts remain below the maximum compensatory height they go on being carried, and oriented, down-wind because they are 'goaded' into persistent flight That may occur only once or twice in a season but can be overwhelmingly important in terms of geographical displacement The sudden, short, but critically important eastward moves in the Arabia-Persian Gulf-Baluchistan area in spring 1943 and 1944 appeared to be brought out partly by these means

Secondly, when the wind begins by being weak, say first thing in the morning, thereby encouraging the locusts to rise high, and then strengthens, it will carry the locusts with it, although without orienting them while they are above the maximum compensatory height This unoriented carriage of high-flying locusts probably occurred during the gale periods mentioned above, and it may be an important cause of with-wind geographical displacement whenever high-flying occurs, as during the evacuation of summer breeding areas

Thirdly, when sudden bouts of strong wind alternate with periods of weaker wind against which fliers can make headway, the resultant movement can be down-wind, even below the maximum compensatory height The function of the periods of weaker wind as contributors to that resultant movement is to ensure that the locusts become exposed to and oriented down-wind by the strong wind below the maximum compensatory height, although they may eventually be brought down by it Sudden lulls in the wind which stimulate taking-off will have the same function This state of affairs was observed in Kenya in 1944 (pp 183, 202) The swarms were observed usually flying up-wind, although often with difficulty, and this meant a variety of flight directions owing to the variable winds of the broken country The swarms certainly did not give the impression of a steady northward trend, although the prevailing wind at that season is from the south (Brooks & Mirrlees 1932), and the resultant displacement of swarms during the period was definitely in the same direction, as in previous years (Waloff 1946*a*) From observations and from inference the slow up-wind migration flights could not determine the direction of resultant displacement, for during the brief periods of strong wind blowing to north or north-west, the locusts covered disproportionately large distances The up-wind flying in variable directions delayed but did not prevent the northward displacement The main reason for the down-wind displacement was the variability of wind speed The locusts were able to get well into the air during the periods of moderate wind, and were then 'whisked away', oriented down-wind, for some distance before they were induced to settle

Fourthly, consider locusts flying at an intermediate height above the ground, where their retinal velocity reaches the compensatory threshold only when the wind is already strong enough to impose down-wind orientation, but is below that threshold when the wind is weaker and would permit up-wind progress A moderate wind will not orient this swarm But when a gust of air moving faster than the minimum compensatory speed hits the swarm, the locusts will orient down-wind, the more readily if they are dense enough for gregarious reversal to occur (see part I, p 229) When the wind drops again to less than the minimum compensatory speed, it will not cause the locusts to re-orient up-wind Observations of swarms being thrown into confusion and turned down-wind on meeting gusts and storms, or flying persistently down-wind in front of advancing storms (p 202), suggest that this sequence of events may be of considerable importance in rectifying geographical displacements It may have contributed to the with-wind displacement of swarms in Kenya (above)

Thus the wind itself appears to be an important rectifier Its speed and structure, and systematic variations in them, affect the amount and height of flight and rectify the wind's directing influence, causing swarms to shift across the map now with and now against or even across the prevailing wind, or to move hither and thither with but little resulting displacement on the map

Temperature may be a very important rectifier, although further information is greatly needed on this point Hot, sunny weather probably increases the amount of flying done and so reduces the likelihood of the locusts settling when the wind is too strong for them to avoid being carried by it, lengthens the daily duration of flying (which may then extend into the night), and increases the average height of flight whether by inducing the locusts to rise by their own efforts or by creating powerful upward convection currents (Rainey & Waloff 1948) Cool, cloudy weather probably leads to flying at lower levels and for fewer hours per day High temperatures would therefore favour with-wind displacement, low temperatures would favour up-wind flying, often with too little overall displacement to create any major trend (part I, pp 238–239)

Dryness, whether of the air, of the insects or of both, may act in much the same way as high temperature, but its role in the behaviour of Desert Locust swarms is uncertain and seems to be less important than for some species (part I, pp 246–249)

The configuration of the *visible substrate* may produce a variety of rectifying effects The direction of *mountain valleys* may create trends (like the year-round trend along the Ethiopian part of the Rift Valley (Waloff 1946*a*), or the movement up the valleys running north-west in south Iran in spring), by canalizing winds or guiding the insects visually (p 245) or both The change of visible background at a *land-water junction* could act in two distinct ways on the optomotor theory Sometimes, perhaps when the water looks strikingly different from the land (sky reflexion, foam, etc), or when the beach itself forms a conspicuous break in the visual field, the shore can act as a barrier, and swarms coming from inland turn and move along it (p 198) On the other hand, a land-water junction also acts as a wind-rectifier, not through the visual influence of the junction-line itself, but probably because of the absence of visible 'landmarks' on water The shore-line then has a local wind-rectifying effect favouring displacement from land out over the water when the wind is both off-shore and on-shore, as already described (pp 267–269) Wind rectification through failure of wind orientation and height 'control' over water may have important long-range effects as well. Other things being equal, locusts will have a more pronounced down-wind tendency, and will move faster, once they are over the sea than they do over land That may well be one reason why Rainey & Waloff (1948) were successful when they assumed down-wind movement, in interpreting swarm movements over the Gulf of Aden, even if some of their assumed heights of flight were too great

Any other circumstances that eliminate wind-induced background responses, e g night migration, would also favour long-range, with-wind displacement Note that night migrations are reported (part I, p 234) in end-of-breeding-season periods of hot, desiccating weather, periods when swarm displacements are most clearly with the prevailing winds (Rao 1942, Waloff 1946*a*) Such weather can rectify the wind's directing influence, therefore, not only by causing high flying by day but also by causing night flying and so bringing another factor, *light*, into operation.

The *age of the locusts* themselves is a rectifying factor. Young *fledgling* locusts seem to respond to wind in the same way as fully hardened ones, but their physical ability to make headway against it is less (p. 200). This should favour down-wind geographical displacement of fledglings, even when the conditions enable older locusts to maintain an up-wind orientation and hence to show either an up-prevailing-wind trend or no trend at all. It seems to follow that fledglings could never make a major migration movement against the prevailing wind, for when low enough to orient up-wind they are too often grounded by the wind. Given warm, calm periods encouraging them to rise well away from the ground, however, they could be displaced long distances down-wind. This probably accounts, in part, for Waloff's (1946*a*) finding that the down-wind trend of migration among *Schistocerca* swarms in East Africa was most clearly defined when new adult swarms were appearing at the close of a breeding season. Conversely, the displacements of fully hardened older locusts not occupied with reproductive activities, would be rectified up-wind as Waloff also found.

Bearing in mind that all these rectifying factors can operate at the same time in varying degree, it is obvious that the possibilities of trend-creation are rich and varied.

Williams (1930) and Key (1942) have suggested a different form of rectification: that the sense of the insects' reactions to wind may depend upon the temperature or humidity or some other condition of the wind. Key's records, for instance, suggested some preference for the movement against the wind, but an even clearer preference for movement up the geographical humidity gradient. He suggested that a change in the humidity of the immediate wind might reverse the sense of the insects' orientation on the wind. But there is no evidence of a direct reversal of the wind reaction itself, and there is no need to postulate it (part I, p. 248).

An access of moisture in the air causes desiccated *Dociostaurus* to fly, to keep low and orient into wind (Bodenheimer 1944). A change in the humidity can, therefore, reverse the course and tracks of the insects relative to the wind, not by reversing the reaction to wind, but simply by evoking a latent wind reaction or by changing the amount and height of flight. Key's data do not include the details necessary for deciding whether the different humidities of the winds, or their different strengths, or some other differences, were the essential rectifying element for *Chortoicetes*. But the form of rectification considered by him and Williams, in assuming that elements like temperature and humidity effect trend reversals by inducing the insect to reverse its reactions, places all the responsibility for the trend-creation on the insect, an unnecessarily complicated hypothesis as to its behaviour. This theory overlooks the fact that insect-wind relations already provide a basis for trend-creation and trend-reversal, so that elements like temperature and humidity can have a positive but indirect trend-creating influence.

ESSAYS IN THE INTERPRETATION OF ACTUAL MIGRATION TRENDS

Until continuous observations on behaviour and weather have been made we shall not know how far the various suggested rectifying processes are in fact responsible for the migration trends revealed by cartographical methods. Meanwhile, some essays in the interpretation of actual migration trends will serve to illustrate the suggestions made.

Consider first the trends prevailing during the two main periods of the writer's observations, and already tentatively analyzed as far as the wind's own rectifying action alone is concerned (pp. 270 and 271) In Iran in spring, 1943, the displacement of the whole swarm population was northward and north-westward as judged from mapping of the records. The winds were observed to be predominantly from the same quarter, which is normal according to Bauer (1935) The most frequently observed direction of flight was against the wind Instances of sustained down-wind flight in stronger winds were exceptional Although such brief flights are easily missed, it was not thought they were frequent, as the weather was clear and settled and winds seldom strong The whole trend seemed to be due to up-wind movement

The trend of swarm displacement was again northwards in the Kenya highlands in spring, 1944, but otherwise conditions were very different The weather was much less settled Wind directions noted at the time of locust observations were inconsistent and affected by the irregular relief The observations were too few for a good estimate of average wind direction, but according to Brooks & Mirrlees (1932) the prevailing wind is southerly at that season—that is, with the migration trend (Waloff 1946*a*) instead of against it Low-flying locusts were observed moving usually against the wind as in Iran, but there were more cases of flight not apparently related to the wind direction on the ground, reflecting the more disordered state of the air currents The general picture was of swarms frequently changing their directions and tending southwards rather than driving steadily northwards as in Iran Thus the Kenya highlands act as a temporary trap for swarms entering them, not merely because the cool, cloudy conditions reduce flight activity (Waloff 1946*a*), but also because they keep flights low and so confused in direction As in Iran, cases were observed of sustained down-wind flight in stronger winds On these occasions the wind was from a generally southerly direction Although the proportion of total flying time occupied by these with-wind moves was relatively small, only they were capable of creating a geographical trend because movements made during the rest of the time were chaotic or ineffectually up-wind.

Note that the difference between the Iran and Kenya trends—the former against and the latter with the prevailing wind—is attributed to the *combined* effects of temperature and wind structure Skies were clear in Iran, and it was warmer than in the cloudy Kenya highlands If this had been the only difference between conditions in the two places the migration trend should have been more clearly up-wind in Kenya than in Iran The swarms in Iran were often enabled to rise high, probably often beyond visually-responsive range of the ground, by the warm weather during the day Yet they maintained their up-wind orientation because it was not disrupted by gusts or storms The warmth enabled them to fly for many hours daily So their up-wind flight became a major geographical trend, given the steady wind direction Indeed, the very fact that they often rose well away from the ground may have aided their up-wind displacement because they were not grounded by small temporary wind increases The swarms in Kenya were held closer to the ground which ensured up-wind orientation when they did fly, but the wind directions were variable, flying was often interrupted by gusts and daily flying hours were restricted by cold and rain so that up-wind flying did not create a trend against the prevailing wind On the contrary, the cooler, cloudy conditions, given the gusty winds, created a with-wind trend Although the proportion of the total flying time occupied by with-wind moves was small, these moves were nevertheless so rapid and covered such relatively long distances that they were responsible for a resultant, northward, with-wind trend *

It appears, therefore, that, although swarms may spend a great deal of time flying against the wind, this can develop into a long-range up-wind trend of migration only under rather exceptional circumstances The wind must be moderate in strength, otherwise the swarms will advance only to be halted and flung back again, and it must be steady in direction, otherwise they will not advance in one direction The weather must be neither too cold nor too hot, for when it is too hot swarms will rise too high to orient up-wind, or they will fly at night with the same result When it is too cold, movement will be too slow for any trend to appear It is not yet clear how far the migration trends in the spring in Iran and Baluchistan, and in winter-spring in Arabia and north-west Africa, are due simply to flying against the gentle, generally northerly wind, and how far they are assisted by the cyclones that occur at that time (Banerji 1931) Both effects seem to play some part Invasions of Palestine (Bodenheimer 1932), of Egypt (Egypt 1916, Ballard *et al* 1932) and of interior Baluchistan (Rao 1942) seem often to be brought by cyclonic winds and sandstorms On the other hand, the invasion of Palestine in 1929–30 was not aided but halted several times when cold, wet gales blew from the south-west (Bodkin 1931), and steady up-wind flight has been recorded at this season in Sinai (Tristram 1880) and in Iran (see above, also Siyazov 1928) One would certainly expect the cold, flight-suppressing storms of winter-spring to be less effective as creators of with-wind trends than storms in the summer-autumn

The combined rectifying effects of high temperature and locust age are perhaps mainly responsible for the great with-wind migration trends during hot, dry weather when young swarms are evacuating areas where they have been bred on earlier rains (Waloff 1946*a*, Rao 1942) The swarms are very active, and the predominance of with-wind tracks and courses is probably due to the swarms frequently rising—or being lifted—away from the ground in hot weather There is, for example, a dramatic reversal of migration trend, both on the map and in relation to the wind, in parts of north-west Africa in the spring (Donnelly 1947) The reversal is associated with increasing temperature and desiccation and with a change in the age of the locusts concerned In December-May mature swarms move steadily north-eastwards against the prevailing north-east surface wind In May-June the young swarms of the new generation move in exactly the opposite direction, south-westward with the same north-east wind The main migrations of spring-bred swarms are generally with the prevailing surface wind also in eastern Africa (south-westwards), in Iran and Baluchistan (eastwards) and south of the Sahara (westwards) Later in the year, when hot, dry weather returns after the monsoon rains, the migrations of the new swarms are again with the prevailing winds in eastern Africa (north-westwards), India (eastward and south-westward) and south of the Sahara (eastwards)

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* The predominantly northward direction found by Waloff (1946*a*) among the swarm reports sent in by casual observers seems at first sight to contradict our finding of a confused, southward tendency in the same area and period However, the chances of a swarm being reported by casual observers are greatest when that swarm passes over the largest number of observers in given time, that is, when the swarm moves rapidly over a long distance and is fairly well up in the air Reports from casual observers are thus weighted in favour of down-wind movements, northward in this case Reports obtained by observers who are actively seeking swarms and whose chances of finding them depend on the swarms not having moved far from where they were last seen, are weighted in the opposite direction, in favour of the lower, slower, longer-lasting, up-wind movements

However, although the migrations of swarms during hot weather are often with the prevailing surface wind, they may be across or against it, and we have not yet enough information on local weather to attempt even a first interpretation of many of these movements Sometimes they are due to exceptional, non-prevailing winds acquiring especial importance Thus the trend of migration among scattered locusts in the northern Sudan and upper Egypt in autumn 1942 was northwards (Kennedy, in preparation), that is, against the seasonal prevailing wind (Sutton 1925, 1930) Observations on some of the moves made by these locusts showed that the winds actually carrying them were associated with occasional, sharp rain- and dust-storms moving northwards Those locusts were not in swarms and their behaviour was not typical of swarm members, but swarms, too, have occasionally been recorded as moving northward from the Sudan at this season (in October-November, 1927 and 1928), perhaps from the same causes

As a rule swarms evacuate the Sudan-Eritrean monsoon breeding areas eastwards, roughly with the south-west prevailing wind This eastward movement continues after surface winds have become northerly Nevertheless, this later phase is not inconsistent with the heat-rectification hypothesis of these post-monsoon movements, because while surface winds are northerly the upper prevailing wind becomes westerly and the locusts may rise to within the latter's influence under hot, dry conditions

The rapid eastward movement across Arabia and Iran into India observed in spring 1942 and 1943 (part I, p 183) was also across the prevailing northerly wind This movement did not result from the locusts rising into an upper wind differing in direction from the prevailing surface wind The surface wind itself changed to westerly for a few days and was then exceptionally violent, hot and dry The locusts were too stimulated to stay on the ground and effected a prodigious geographical displacement toward an area of summer rainfall, a movement of crucial importance for the further progress of the migration and breeding cycle The temperature, wind speed, wind structure and perhaps also the dryness of the air, all probably conspired to rectify the locusts' movement down-wind in a spectacular manner Before and after this short period they were migrating steadily northward in Iran, and went on doing so into the summer, although unable to breed and destined to disappear there Faure (1894), Regnier (1926) and Bodenheimer (1932) are among those who have also spoken of Desert Locust invasions being brought by winds that were both hot and violent

One quite exceptional migration movement has been interpreted in the light of the detailed meteorological situation by Waloff (1946*b*) This was a rapid movement of *Schistocerca* swarms from the westernmost point of Africa (south of Agadir) to Portugal and Spain in October 1945 She suggested that the high temperature over the land at the point of origin enabled the swarm to rise to 1500 to 2000 ft , where there was a 30 m p h southerly wind capable of carrying them to Portugal in the time available She suggested that their estimated average speed of 23 to 28 m p h could not have been achieved at the surface because the wind there was generally less than that speed It should be pointed out, however, that if the locusts were oriented down-wind they might have maintained the necessary average speed even at the surface Moreover, if they were down near the water in daylight in a wind too strong for them to make headway, they probably would in fact be orientated down-wind, especially if dense enough for gregarious re-alinement to occur

Bearing in mind that swarms have been said to average only 20 to 30 miles a day over land, Waloff suggested that it was simply the act of flying high in the rapid wind which enabled the locusts to cover so great a distance in one day or so Another reason that may be suggested for the locusts flying so far and fast was that they were over the sea, and not over land It seems probable that the high temperatures over the land enabled the locusts to rise high and so cross the coast, but there is no evidence that they remained high throughout their long journey The locusts were reported in Portugal mainly near the coast itself They were flying now southwards, against the wind This also suggests they were low before reaching land and had changed their behaviour on arrival over land simply because they could now see the substrate's apparent movement It is not apparent how descent could have been induced merely by a decrease in wind strength, as Waloff suggested

The above analyses are tentative What is required is the study of individual trends according to the actual weather at each time and place Without more information it is not possible to offer even tentative explanations of some well-defined across-prevailing-wind trends, like the north-westerly movement across the Sahara in October-January which occurs when the prevailing surface wind is north-east

Nevertheless, the various 'rectification' hypotheses do show some promise as means of interpreting actual migration trends The immediate conclusion from these interpretative essays is that the great migration trends, which are roughly with or against the prevailing wind, emerge from the mesh of migratory movements *only when several rectifying influences are acting together in the same sense*

Discussion

'*Active*' versus '*passive*' *migration*

The theory advanced here attributes long-range movements to both insect and wind acting together Most writers on insect migration have sought rather to separate the action of the insect from that of the wind They distinguish active or 'voluntary' migration from passive or 'involuntary' migration This conception has been carried to the extreme by Acworth (1940), who divides all insect (and bird) migrations into two neat stages, an outward drift on the wind followed by an active 'homing' flight Acworth's simplified theory has won little support, but the distinction between active and passive migration is made also by Williams (1930), who regards passive migration as typical of some insects, but takes the view that it should not then be called migration The term migration he would reserve only for the active (that is, powerful) migrants, such as butterflies, dragonflies and locusts He does not say that the displacement of true migrants is invariably due to their own exertions but, even when it is passive, he regards it as under the continuous control of the migrant

> 'The movement is produced, to some extent at least, by the efforts of the migrating animal, which is neither a passive victim of overpowering external forces nor an active objector to them '

And, more specifically.

> 'The migrating animal is in some way conscious of, and helps to determine, the direction of movement'

Thus the view that migration is essentially active has been developed into a theory of consciously directed movement

Analysis of the behaviour of migrant locusts (part I) shows they are subject to an internal 'drive' that makes them fly, but that this is not a geographically directed drive The most decided trends of locust swarm migration are with the wind and appear when the locusts have *least* behavioural control (in the objective sense defined on p 266) over their own displacement over the ground their main contribution is to keep flying Vice versa, trends become confused or even disappear when the locusts have nearly complete control over their own displacement A major trend can occur under the behavioural control of the locusts, but only, it is suggested, against the wind Such a trend is not executed in spite of the wind, but is created by it

Moreover, it is the 'uncontrolled' migration trends that are usually 'successful' in the sense of leading to new breeding grounds, while the controlled ones are sometimes 'abortive' (p 276) And migration goes on even among sexually exhausted swarms until they die out (part I, p 200) It is impossible, as Uvarov (1928 *et seq*) has always insisted, to entertain the idea that migrations are directed to a goal

In his more recent writings, Williams (1942, 1949) no longer suggests that the theory of an innate sense of direction can be the basis for further work He believes (1949, p 84) 'the answer will be found in the field of biology and physics', and that there is 'a mystery in the sense—and only in the sense—that we have not yet found the answer' Nevertheless, he adheres to his sharp distinction between active and passive migration, and gives this new definition of the former (1949, p 70)

> 'A change of location which is determined both in distance and direction by the insect itself, and not a passive distribution of individuals by overpowering forces such as strong winds'

On this definition many of the most spectacular long-range movements of locusts—movements, moreover, which are of crucial importance for the completion of their annual breeding cycle—are not migrations at all, because the wind probably contributes more than do the locusts to their actual displacement over the ground But, as we have seen, it is only because the insects take to the air so persistently and react in various definite ways that they so commonly expose themselves to carriage by the wind, and by winds from some directions more than by others Getting into a position to be so carried must be included among the means by which migrants determine—in an objective sense—their own displacements both in distance and direction, along with other means such as orientation During the period of carriage by the wind, the insect's displacement is certainly passive from the point of view of a fixed ground observer But the movement as a whole is nonetheless self-directed in the objective, resultant sense, and if that kind of self-direction is to be excluded by definition, then what remains can only be some kind of subjective, conscious self-direction

The contrary theory, that long-range migration is essentially passive, has been put forward by Felt (1928, 1938) ·

> ' winds, especially those of the upper air, are ample to account for the occasional and possibly somewhat general extended movements of insects There is no necessity for limiting such movements to species possessing superior flying ability since the probabilities are that the purposive flight of an insect—the distance covered by its own efforts—is relatively insignificant' (1928, p 123)

There is an attractive mechanical simplicity about this theory, which discounts (without having to deny) a purposive element in migration, and seems to justify treating the insects, for working purposes, as inert particles Attention is thereby shifted from the behaviour of insects to the behaviour of air-masses Yet migration remains a biological problem which cannot be solved in primarily physical terms

More important than the difference between the 'active' and 'passive' theories of insect migration is what they have in common the assumption that active and passive migration are alternatives The one theory holds that a movement is not a true migration unless the insects are in complete control of it, the other holds that insects rarely have any control over their long-range movements which must nevertheless be admitted to be migrations More commonly, perhaps, these two extremes are avoided, as by Fraenkel (1932) and Freeman (1945), but the sharp distinction between the alternatives of active and passive migration is still retained

> ' a rich aerial fauna, consisting of weak-flying insects of small size and high buoyancy These forms, being carried involuntarily by the wind, are dispersed by air movements as contrasted with the migration of moths, butterflies and locusts, which are sufficiently powerful to maintain their flight if necessary against the wind' (Freeman 1945, p 150)

What seems to be under-emphasized here is that long-range movement, no matter to what degree controlled *en route*, rarely occurs unless the insects' behaviour contributes in some positive way to it, and that it is the making of this contribution, not the mechanism of their horizontal displacement, which distinguishes the insects biologically as *migrants Displacement* may be active or passive, but 'passive *migration*' is a contradiction in terms

There is, in fact, wide variation in the degree to which migrants traverse the ground through their own exertions, or on the wind The variation is continuous and its causes need to be studied, whereas it tends to be left on one side when migration is regarded either as essentially active, or as essentially passive The antithesis between 'active' and 'passive' migration is misleading, for it gives primary importance to a biologically secondary matter the particular *means* of traversing the ground, employed by migrants

In any given case the antithesis is even more misleading, for activity and passivity are not alternatives The study of locust migration has suggested that the wind is an essential element in the creation of any geographical trend among numbers of swarms As long as we are considering such trends, and not the momentary behaviour of a single locust or a single swarm, there is no point at which we can say the insects are now active, or now passive They are always both active and passive Swarms can suffer the passive displacement that is the basis of a with-wind trend, only by becoming and remaining actively air-borne Swarms can accomplish the active displacement that is the basis of an up-wind trend, only by suffering and successfully overcoming passive carriage by the wind It is never either the locusts or the wind that creates a trend It is their conflict which is the basis of trend creation, third factors creating trends by influencing its outcome

Migration as a complex of interacting factors

Locust students have not, on the whole, been attracted by the 'passive' theory of migration, for they have adequate evidence against it, despite the clear evidence of the wind's importance in long-range locust migrations They have been even less attracted by the 'active' theory of goal-directed migration, and have emphasized its complete incompatibility with their evidence But they have not hitherto produced any general theory in place of those they reject, although the material at their disposal is richer in quantity and quality than the material on any other group of insect migrants Gunn *et al* (1948, pp 43–44) have even gone so far as to say

> 'The plain fact is that these gregarious locusts migrate in swarms and nothing is known of the causes '

This was, perhaps, a deliberately exaggerated statement made in order to counter the speculative approach of Heape (1931) But what it implies is that the whole matter is extremely complex, and the best policy is to wait until all the multifarious factors have been unravelled A preliminary attempt to do that has been made in this and the preceding part The conclusion is that we are not, after all, dealing with a complex system of 'interacting factors' In essence, the system is simple

However fluid and complex the migrations and however many factors might be involved, it was known that order did emerge from the chaos, as a recognizable pattern of trends bearing some relation to seasonal winds It was plain from everyday observations on locusts and many other insects that they resist carriage by the wind when in a position to do so These two pieces of information together were basis enough for a first working hypothesis essentially the same as the theory of trend-creation now advanced after much additional work But they were not so put together by anyone (including the present writer), it seems, because the numerous factors involved were regarded as all of similar rank, although not of similar weight, in their influence on the situation The tendency was to consider the various factors as interacting, but all direct influences in their own right, demanding patient, piecemeal analysis, without preconceived ideas

This 'factorial' approach, with its technique of multiple regression, has led to discoveries as in the work of Gunn *et al* (1945, 1948) on mass departure of swarms in the morning But the same work showed that main reliance on this approach can mislead the discoverers, when its conventional treatment of events as the product of interaction between directly participating, self-contained factors is projected back into the events in nature In reality factors like temperature seem to participate in mass departure only indirectly, through their effect upon the relations between individuals, or, more precisely, through their effect upon the rivalry between the individualist and gregarious tendencies of each insect (part I, p 230)

It seems to have been a similarly mechanistic concept of interaction (and again with the employment of mainly statistical methods) which led to Key's (1942) suggestion that temperature or humidity may reverse locusts' orientation to the wind (p. 278) The temperature or humidity are here assumed to act directly on the insects, reversing their orientation responses to wind This rather elaborate behavioural hypothesis is unnecessary, since the insects' courses and tracks can be reversed simply by changing the height and amount of flight There is also evidence (Bodenheimer 1944) that the appearance or non-appearance of wind orientation (but not its reversal) can itself be controlled by air humidity, possibly through changes in the height of flight, which would again help to bias movements up- or down-wind Thus trends can be reversed without the whole behaviour being reversed, because factors do not act directly or on their own, but in a context, in this case, on an unstable system which itself produces reversals when interfered with

Williams (1930), while holding the view, rejected by locust workers, that migrants may be guided by an innate sense of direction, nevertheless gave careful consideration to the above hypothesis of long-range direction-determination by direct reversal of orientation to wind [*] He shares the mechanistic view of the possible mode of action of external factors, and has merely taken it to its logical conclusion, in the theory of an innate sense of direction How close to that theory even its intended opponents can come is seen in the final clause of this statement from Gunn *et al* (1948, p 44)

> 'Observation at this stage (stream-away) might therefore provide some indication of the stimuli responsible for the locusts adopting a particular direction, if indeed external stimuli play any part at all'

Williams has been equally concerned to find external agencies that might determine the direction of migrant insects and was associated with the experimental study even of a rather unpromising agency, the earth's magnetic field (Cockbill 1942)

> 'I do not think that magnetic polarity is likely to be the cause of orientation—although it is an attractive theory ' (Williams 1949, p 82)

Magnetic orientation seems an attractive theory only so long as one regards agencies as self-contained, exclusive, direct influences upon the insect, and if, therefore, one's aim is to find some one agency which could guide the insect unremittingly throughout a long-range migration Since no agency has yet been discovered which seems capable of acting in that way, Williams calls for still further search, and never entirely abandons his alternative explanation an innate sense of direction There is, indeed, no third alternative when the environment is regarded as a congregation of self-contained, directly (i e reflexly or mechanically) acting factors It is incredible that such factors would be capable, singly or jointly, of creating a regular pattern of migrations They are all too inconstant

Once again, two seemingly opposed theories turn out to be complementary the one regarding migration as consciously directed and the other regarding it as mechanistically directed They meet on the common ground of factorial analysis When the objective approach becomes a purely factorial one, it takes on so strong a bias against having any bias that it leaves an inviting vacuum for subjective theories to fill

The weakness of the factorial approach lies unnoticed in the very concept of a factor No matter how much interaction between factors may be recognized, they remain, in this conception, self-contained things, like so many billiard balls. Billiard balls can be imagined as having different sizes and weights and as associated in various ways, but they remain discrete, self-consistent things with one set of properties each When natural forces are thus isolated in thought to distinguish their properties, and then, so to speak, put back into nature by the investigator to see how they interact, they often appear to him still as isolates self-contained, self-consistent and incapable of behaving in two ways at once

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[*] He went on to reject this hypothesis, but for reasons (see part I, p 249) which do not affect the present argument.

A natural element, when regarded as a *factor*, is something that varies in quantity *but not in quality* In order to assess its influence, it is thought sufficient to measure it, and correlate the measurements with the biological events under study But it is only in idealized isolation that the wind, for example, may be characterized adequately by measurements As an *influence* it varies both in quantity and quality The changes in the quality of this influence which come with changes in its quantity, or with changes in the natural context, are the core of the problem

For example, the concept of self-contained, interacting factors obscures the dual role of the wind in direction-determination The wind is an element in the central system of locust *versus* wind, yet it is at the same time a rectifying element acting upon that system (p 270) The quality of the wind's influence in trend-creation varies also with the age of the locusts To see the influence of a factor it is necessary not merely to measure it, but above all to see the context, otherwise the measurements can even obscure its role

In our case where displacement of the insects can occur only through the action of two opposed factors, insect locomotion and wind carriage, the other external factors can become influences only as they are focused, as rectifiers, on that antagonism Even then, the amount and the kind of influence each has, will depend on the others and on the locusts If such preconceived ideas be admitted, then it becomes possible to suggest a theory of long-range trends without first dissecting out and measuring every element in the complex system and, equally, without abandoning objective analysis by introducing the idea of an innate sense of direction A trend is not imposed by any external factor but is something new, created by a system in which external factors are causal elements

The ecological character of long-range migrations

Increasing attention has been given in recent years to the many types of orientation reaction displayed by insects (Fraenkel & Gunn 1940), and this has made itself felt in discussions on migration It has emphasized the possibility that several reactions, rather than any single one, determine the orientation of migrants (Kennedy 1948, Gunn 1948*b*, Williams 1949) Williams conceded the possibility that the migrating insect might 'orientate at one time by the wind, at another by the sun—and so on', but could see no basis on which the insect's several reactions could be organized into a long-range directional movement, unless it were the insect's own wishes That conclusion being unacceptable, Williams rejected all known types or combinations of reactions as irrelevant to the problem and appealed for more and more work until the cause of orientation should one day be discovered Gunn (1948*a*), on the other hand, supporting the idea that migrants are directed by means of more than one reaction, drew attention to the principle of 'multiple assurance' in the maintenance of an upright posture by man, where proprioceptors, pressure receptors, eyes and labyrinths are all used, each of which is adequate by itself

Neither Gunn nor Williams, however, drew a clear distinction between short- and long-range movements, when discussing how their directions might be set Unless this distinction be clearly drawn, citation of the principle of multiple assurance may be taken to mean that what is 'assured' by the migrant's multiple orienting reactions is its long-range direction, just as a man's posture is assured by his multiple righting reactions Williams (1949, p 84) understood the principle in this sense, and his objection, that this amounts to saying the insect knows the direction in which it wishes to go, is perfectly valid, for how else could the insect's multiple reactions be made to assure one certain direction, for hundreds of miles on end?

But posture-maintenance and long-range direction-determination are not parallel cases The migrant insect's reactions are not co-ordinated by its nervous system in such a way as to maintain a constant direction over long distances, as a man's reaction-pattern is co-ordinated to maintain his upright posture The migrant's reaction pattern is co-ordinated in such a way as to do something simpler and more immediate (like posture-maintenance), viz to maintain the sensed environment as constant as is compatible with the migrant's own persistent locomotion In maintaining that kind of equilibrium, 'multiple assurance' creates the short-range constancy of direction so characteristic of large migrants (part I) The migrant cannot avoid continuous change in its environment The best its central nervous system can do toward achieving sensory stability in many circumstances is to keep a straight course, because the changes to which the insect can respond without halting are due principally to its own deviations from a straight course, which produce sudden changes in its relation with the more constant features of its environment Its reactions are therefore selective in the sense that it reacts to certain more constant environmental features and 'ignores' many incidental features of its moving, panorama environment

Long-range trends seem to be created quite differently We know of no environmental feature so constant over long distances that the insects could keep going straight by long-continued, sensory-stabilizing reactions to it Nor do we need to look for one, since we have no reason to suppose that long-range trends involve flying straight all the way The basis for organizing the insects' orienting reactions and displacements into a long-range directional movement is not the insect's central nervous system According to the theory advanced here, it is the environment that selects certain of the insects' reactions (to wind, particularly) and creates resultant trends by means of rectification, while the other orienting reactions make little or no contribution to long-range direction-determination The large-scale orderliness of the environment, which is of a kind that does not exist on a small scale, is the basis on which the migrants' movements become organized into an orderly pattern of long-range trends But the environment always acts through the insects' orienting and other reactions many of which are well known, so that all known reactions cannot be treated as irrelevant to the problem

The theory of an innate sense of direction, and the principle of 'multiple assurance' if applied to long-range directional movements, both assume these are linear extensions of short-range directional movements The two theories differ, of course, in that the first minimizes the directing influence of the environment while the second insists on it But they are at one in seeking to explain the directions of both short and long movements in behavioural terms On the contrary, for locusts at any rate, the fixity of direction seen in short-range movements, and the consistency of direction seen in long-range trends, appear to be different things, differently created The long-range trends cannot be explained in behavioural terms alone They are events on a higher plane than behaviour ecology The laws governing the creation of long-range trends, and their organization into a regular pattern, are intrinsically no more elaborate than those governing behaviour, but they are quite different They are ecological laws, in the sense that they arise from the interaction between a whole population of insects and a whole system of climatic and geographical circumstances The environment enters into behaviour, one might say, as weather and terrain, but into large-scale migration, as climate and geography

Migration of other insects

How far the principles suggested here may apply to the long-range migrations of other insects is a matter for investigation The object of the following remarks is simply to indicate that there is nothing in the evidence known to the writer concerning other insect migrants, which would rule out the extension to them of the general principle of 'rectification', and the consequent distinction between the behavioural and ecological levels of migration analysis Apart from the fact that some of the alternative theories criticized here have been applied to locusts and butterflies alike, there are already indications that the principles governing butterfly migration may not be as remote from those suggested for locusts as has been supposed

First, Wiltshire (1946) has pointed out that Lepidoptera migrations, when observed within their 'geographical headquarters', follow a complicated pattern

> 'The general picture is one of travel in many directions under environmental stimuli and of temporary or permanent settlement wherever the environment permits '

The over-simplified picture of an emigration followed by a return as the set pattern of butterfly migration arises, in Wiltshire's view, from the fact that most observers of Palaearctic butterflies reside, not in the headquarters region of these species, but at the extreme edge of that zoogeographical zone

Secondly, the records already assembled by Williams (1949 *et ante*) show a clear preponderance of migrant butterfly flight directions against or with the wind rather than across it This he dismisses as mere coincidence, or as due to a 'psychological error' on the part of observers It must be admitted that such crude statistics are not reliable evidence of any real preference on the part of the migrants But neither are they evidence against the existence of such a preference The data, aggregated without regard to the varying and often unrecorded circumstances at the time of observation, do not permit any allowance to be made for wind speed and height of flight This procedure would conceal the sort of consistency in flight direction-wind direction relations found with locusts What can, therefore, be safely said is that the available data in no way exclude the possibility of the wind having an important influence on the direction of butterfly migration, but an influence that changes according to the circumstances as with locusts. The mainly statistical approach to butterfly migration in relation to wind—the amassing of occurrence records—has deferred rather than brought nearer the discovery of the causal connexions involved (part I, p 205)

That is not to say that we can expect to find no important differences between butterflies and locusts For example, it seems that butterflies customarily retain more control than locusts do over their own displacement, by more often avoiding flight in strong wind, keeping closer to the ground, and so on During the southward migration of *Pieris brassicae* L at Harpenden in 1940, which continued on every fine day for several weeks during which the wind blew from almost every quarter, Williams (1942) remarks that 'the only noticeable effect (of the wind) was that when it was strong a *few* butterflies seemed to be carried away with it against their inclination *and usually high in the air*' (my italics—J S K)

> 'Nearly all butterflies when on migration tend to fly at the height which is normal for non-migratory flight, most individuals are below 10 feet, and few more than 20 feet above the ground, or above the tree tops if over forest land' (Williams 1949, p 74)

Williams (ibid) goes on to quote striking examples of the way butterflies regulate their height, moving up and down at a constant height over an uneven substrate

The fact that butterflies keep closer control over their own displacement than do locusts, does not exclude the possibility of their migrations being directed *in the long run* by the wind If closer control over their own displacement means less dependence of course and track upon the immediate wind, it also means there will be more chance of any given course, once set by an orientation reaction to the wind, or to any other agency, at a critical time such as at the start of migration in the morning, being maintained for hours afterwards when the migrants have ceased to orient to that agency (cp p 270) And the fact that butterflies have been seen flying equally often with and against the wind does not mean that they cover equal distances with and against the wind, i e that the two orientations are equally important in long-range migration An example of short-range wind rectification, in Monarchs (*Danaus plexippus* L), has been quoted on pp 267–269 A more generally interesting example of wind rectification has been recorded for the Silver-Y moth, *Plusia gamma* L , in Denmark (Larsen 1949) The species sometimes migrates by day, when its directions do not show a regular relation to the wind direction (Williams 1949) But Larsen observed it migrating at night, when its displacement was consistently with the wind, the light (or rather the lack of light) perhaps rectifying the displacement down-wind (cp p 272)

If locusts exercise less control over their own displacement than do butterflies, the smaller, weak-flying insects such as aphids obviously exercise far less control than either locusts or butterflies Aphids commonly rise to great heights, and their long-range movements are effected, in the narrowly mechanical sense, entirely by the wind (Fraenkel 1932, Glick 1939, Hardy & Milne 1938, Freeman 1945) But in what conditions of wind, temperature, light, etc , they take off and alight is governed by their own active behaviour (Davies 1935, 1936, Broadbent 1949) The main difference between them and the larger migrants is the relatively small contribution they make to their actual displacement over the ground This difference is a merely quantitative one as far as behaviour is concerned, and provides no grounds for placing small insects like aphids in a separate behavioural category of passive migrants, distinct from a category of active or true migrants (cp p 279, and Kennedy 1950) In making their long migrations aphids require to be carried by the wind, but third, rectifying factors decide the direction, speed and extent of such movements by determining, through the insects' reactions, in what winds and for how long they fly

There are other possibilities to be borne in mind which do not necessarily involve the wind. Lindroth (1948), for example, made observations which suggested a way in which the long-range migrations of Carabid beetles might be directed by the sun through positive phototaxis The mornings being too cold and day-times too windy, the beetles took off toward the sun mainly during warm, calm evenings and so flew westward, which is in accordance with the distributional evidence of their westward movement over the sea in spite of a prevailing south-westerly wind In the terminology employed here, this westward trend would be ascribed to temperature and wind rectifying the primary directing influence of the sun This example illustrates once again how the possibility of some environmental feature being responsible for the direction of a long-range movement cannot be dismissed simply because that feature's own direction varies

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EXPERIMENTS ON BIJUGATE APICES

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(*Received* 19 *April* 1950—*Revised* 14 *October* 1950)

The bijugate phyllotaxis and the shoot apices of seedlings of *Dipsacus laciniatus* are briefly described and discussed The normal mean angle between successive pairs of leaves was found to be 72° 7

Experiments are reported which were designed to test a suggestion that in bijugates the deviation of each new pair from a position at right angles to that of the previous pair is due to an inhibition from the second older pair below The leaves of the apical buds were removed as far as the youngest pair (the P_1's) inclusive, or as far as the P_2's or P_3's only After the operations the angles between successive pairs increased considerably, and the increases continued for five or even six plastochrons Also some angles increased beyond 90° and reversed the spirals It is pointed out that these results are difficult to reconcile with the inhibition hypothesis

Comparison is made with the bijugy of apices of *Salvia horminoides*, which can be explained junctionally as due to the contacts 1, 1 and 2 of the leaf bases

For the bijugy of *Dipsacus* an explanation is suggested in terms of the combined working of two factors The first factor is junctional and depends on the shapes of the leaf bases with their united rims The second factor is a pressure exerted by the upstanding parts of the P_2's on the sides of the stem apex, which they were seen to touch The results of the experiments can also be understood on this basis

1 INTRODUCTION

In the simplest bijugate phyllotaxis it can readily be seen in bud sections that the young leaves are arranged in pairs of opposite members, just as in the common decussate phyllotaxis, but that the plane of each pair is not at right angles to that of the previous pair For each of these planes deviates a little from the right angle, often from 10 to 20° (figure 1), and these deviations are all in the same direction in any one bud, though not in different buds of the same plant Thus the arrangement is both paired and also spiral It is therefore not possible to draw one genetic spiral through all the leaves in their order of formation, as it is in simple spirals, but one can draw through them two parallel genetic spirals, of which each one passes through one leaf of each pair This simple bijugate phyllotaxis is regular and characteristic in the rosette stages of the Dipsacaceae, and is found in the rosettes of a few species of other families (see figure 17, and Church 1904, p 167) It undoubtedly exposes the leaves of these rosettes to light much better than would straight decussation, which is rare in rosette stages and seems very unsuitable for them In the rosettes of *Dipsacus* each new pair of leaves makes contact below it with the next older pair only

Later in the growth of the Dipsacaceae, when the buds have elongated and begin to form the inflorescences, the arc covered by each lateral member diminishes, new contacts are formed, the phyllotaxis rises and parastichies become conspicuous The numbers of these parastichies, or spirals of two sets passing through the lateral members and winding round the apex or axis in opposite directions, are commonly twice those successive numbers of the Fibonacci series which are found in simple spirals (see Church 1904, chapter 17 and illustrations), and the divergence angle along each of the genetic spirals (as distinct from the steeper parastichies) comes very close to 68°·5, or half the Fibonacci angle of 137°, as was pointed out by the Bravais (1837) This can be verified on figure 74 of Church (1904). The lateral members are still paired, but the pairs are less conspicuous

The way in which these higher bijugate systems are developed from simple bijugy as the arcs diminish and the contacts change seems to present no *special* problem, but to be quite similar to the ways in which simple Fibonacci spirals are developed from distichy and from straight decussation, of which van Iterson (1907) has given much the best account But the simple bijugy itself does present a special problem, and the present paper will be concerned with an attempt to discover its causes

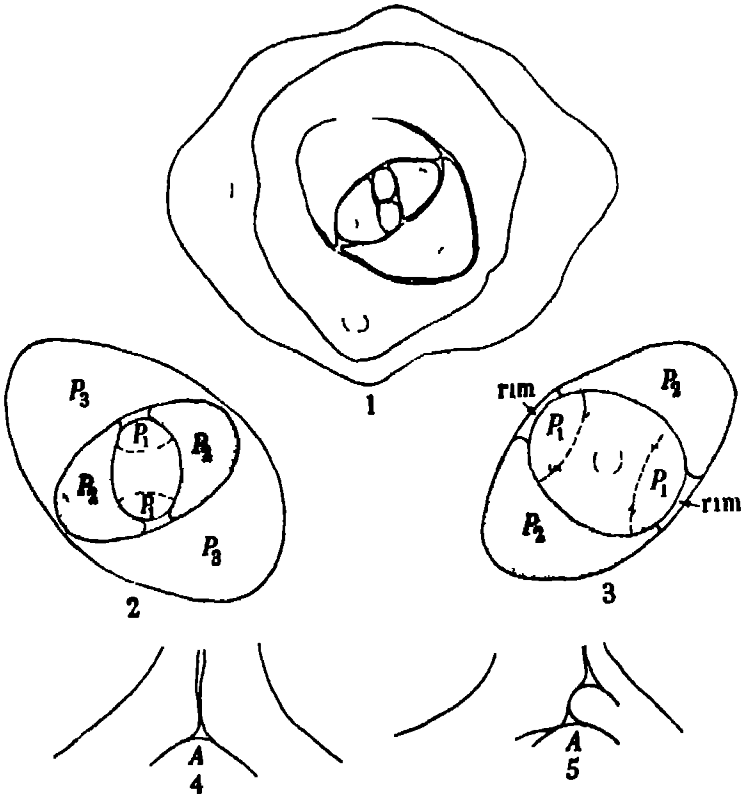


FIGURE 1 *Dipsacus laciniatus* Cross-section of normal bud (magn ×17)

FIGURES 2, 3 Normal apices exposed, diagrammatic The P_1's and P_2's have been cut down

FIGURES 4, 5 Normal apices in longitudinal section (magn ×40) Stem apex is marked *A*

Church (1904) has indeed tried to apply to bijugy his 'parastichy' theory, according to which the leaves are determined at intersections of the parastichies of the two opposite sets For this purpose he points out that through the leaves of a rosette of *Dipsacus* one can draw two opposite sets of spirals, which he calls the parastichies, one set containing two spirals and the other four, and that if the numbers of both sets are even, then the phyllotaxis must be bijugate But a weakness of this interpretation is that along the spirals of the set of four the bases of the youngest leaves are not in contact, in *Dipsacus* at least, as the writer finds, so that it seems arbitrary to select these spirals and consider them causally significant. (Church's drawings, figures 62*a*, *b*, do not show the contacts of the youngest leaves) In any case Church's whole parastichy theory (1904) can hardly be considered to be a clearly worked-out causal theory, whatever may be its value as a system of geometric constructions imitating phyllotaxis Church has, however, contributed many valuable observations and drawings of the higher bijugate systems of the inflorescences of Dipsacaceae

It is also difficult to explain the simple bijugy of rosettes of Dipsacaceae on the basis of any junctional theory of phyllotaxis, if the term 'junctional' introduced by Schoute (1913) may be used for any theory according to which the positions of new lateral members depend on the existing members directly neighbouring to them For in *Dipsacus* at least, as the writer finds, each new leaf makes contact with the members of the next older pair only, so that on junctional grounds a straight decussation would be expected unless there were some special complicating factor Recently, however, Richards (1948, p 231) has made a suggestion to explain simple bijugy which goes beyond a purely junctional theory He supposes that the positions of any new pair of leaves *n* are modified by inhibitions or repulsions from the second older pair *n*–2 below them, although the leaves *n* never make contact with that pair, but are separated from it by the flanks of pair *n*–1 (see figure 2) These inhibitions cause the plane of pair *n* to deviate a little from the plane at right angles to *n*–1, and when once these deviations are started they will clearly continue in the same direction Such a process would be important, if genuine, and the suggestion attracted the writer very much, especially since for several years evidence had been accumulating that in *Rhoeo discolor*, a monocotyledon with spiro-distichous phyllotaxis, the new leaves are indeed repelled in a similar way by older leaves with which they do not make contact (Mary Snow, 1951), and spiro-distichy is related in form to straight distichy rather as simple bijugy or spiro-decussation is to straight decussation

In *Lupinus albus*, indeed, we concluded that the position of a new leaf is not appreciably affected by any other existing leaves except those with which it makes contact (Snow, M and R 1931, pp 17, 27, 1933, p 377, 1947, p 15) But it seemed possible that in the Dipsacaceae, with their peculiar phyllotaxis, a different factor might be at work, as it is in *Rhoeo* Accordingly the writer has experimented by operating on shoot apices of *Dipsacus laciniatus*, and these experiments and various observations will here be reported and discussed

2 THE NORMAL APICES AND PHYLLOTAXIS OF *DIPSACUS LACINIATUS*

Since the leaves of each pair are fairly accurately opposite, the divergence angles were taken to be the angles between the median planes of successive pairs, which are simpler and easier to measure than the separate angles along the two genetic spirals (see figure 1) Thirty angles were measured, in sections of apical buds of eight plants pickled at about the same stage as at the end of one of the experiments to be reported The mean angle was 72° 7 The standard deviation was 3° 61, and the standard deviation of the mean was 0° 66 The extremes were 68° and 80° The apical part of the axis, apart from the actual stem apex or apical cone, is slightly crater-shaped, so that even the older leaves of the bud are cut close to their bases in cross-sections just above the stem apex, and show the divergence angles accurately

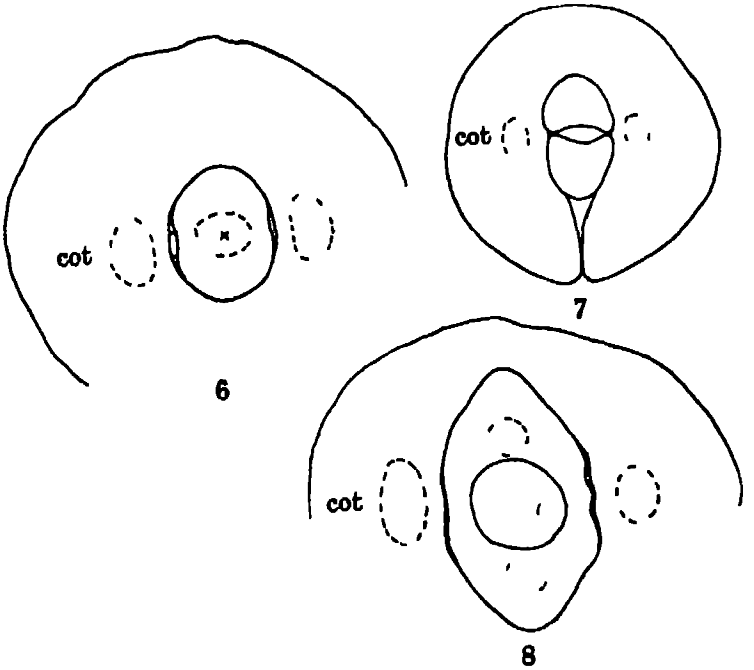
On the other hand, the sections through the stem apex did not show clearly the shapes and relations of the stem apex and youngest leaves For the apical cone and the youngest pair of leaves, or their bases, appeared only indistinctly, rising up from a nearly flat disk of tissue which formed the background, and the next older pair were often inserted at a higher level and did not appear in the same section More instructive therefore were observations of this region in the solid made with a Leitz Greenough binocular at magnification × 50 or × 75 giving stereoscopic effect, and observations of this kind were made whenever the P_1's or young P_2's were removed in an experiment (The P_1's and P_2's are the youngest and second youngest pairs of leaves visible at the time of operation, and the pairs arising after the operations will be called the I_1's, I_2's and so on, as before)

In some ways the apices are similar to those of decussate species, except of course that the divergence angle is not 90° (see figure 2) For each new pair of leaves arises from the narrow ends of a stem apex which seen from above near the end of a plastochron appears elliptic, except that the narrow ends often look a little flattened and after this the remaining stem apex is extended transversely to form an ellipse in the other direction Also the youngest pair makes contact at its base with the next older pair only, as in decussates But in *Dipsacus* a striking point is that the leaves of the youngest pair unite by low rims at the end of the plastochron, as was noticed several times These rims can be seen in figure 3, which, like figure 2, shows the appearance of an apex in which the P_2's and older leaves have been cut down The shaded areas represent the cut surfaces of the P_2's, and the P_1's are just arising The P_2's are here the youngest pair with united rims, since the plastochron is at an early stage

Another point of interest is that the upper parts of the youngest leaf-pair but one (the P_2's in the experiments) bulge forward between the youngest pair, and at about mid-plastochron they touch the apical cone or stem apex over a considerable area, though they do not quite touch its extreme summit These contacts are illustrated in figures 4 and 5, as seen in longitudinal sections Also observations of apices in the solid often revealed this process, and showed that the P_2's already touch the stem apex at the beginning of the plastochron Indeed in one plant a pair of old P_1's was found to be already touching the apex The contact of the P_2's with the apex reaches closest to its extreme summit at about mid-plastochron, and later the bulging part of the P_2's is carried up away from the apex, and the P_1's curve forward and meet beneath it at their tips Further, when a pair of P_2's which touched the apical cone was removed by being pressed outwards, as will be described, they sometimes left a nearly transparent film of some kind adhering to the apical cone (figure 3), so that these leaves must actually have been pressing on the apical cone and adhering to it slightly These films were of course quite distinct from the remaining bases of the leaves removed, and their upper boundaries, towards the summit of the apical cone, were seen as brown lines, and showed how far up the apical cone the contact of the P_2's had reached The brown lines are represented in figure 3 by the lines of dashes drawn cross-wise it can be seen that they reach up the stem apex almost to the little apical dome which is conspicuous when the plastochron is at an early stage, as it was in this observation These contacts of leaves with the stem apex are unusual, and may be characteristic of Dipsacaceae The significance of these contacts and of the united rims will be discussed in § 5

The start of the bijugate phyllotaxis in seedlings is also of interest In sections of fourteen seedlings, only just germinated, the first divergence angles, those between the cotyledons and the first leaf pair, were found to be very close to 90°, having a mean value of 86°·6 (see figures 6, 7, 8) The lowest two were 83° and three were exactly 90° But the second divergence angles were found in eight young seedlings to have a mean value of 71° 1 (extremes 62 and 84°) With the second angle the deviation of the phyllotaxis is established, and it then continues in the same direction But the small deviations of the first angle from 90° must be accidental only, since they were found to be often in the direction opposite to that of the second and subsequent angles, as in figure 8

These points need to be observed in bud sections for in the intact seedlings it looks as if the first divergence angle regularly deviates from 90° considerably and in the same sense as the subsequent angles But this is apparently because the blades of the first pair of leaves shift by lateral curvatures from under those of the second pair Thus in two of the above seedlings in which the first angles were seen in sections to be 89° left and 90°, they had both been estimated on the intact seedlings as 70° right



FIGURES 6–8 Bud sections of very young seedlings (magn 6, × 47, 7, 8, × 40)

In the axillary buds the development of the bijugate phyllotaxis is difficult to follow, since they are very much flattened when young, apparently by pressure from the leaves above and below them, and their phyllotaxis is thereby made irregular and abnormal

3 THE NATURE OF THE EXPERIMENTS AND THE METHODS

In order to test the suggestion of Richards, the developing leaves of rosettes of *D laciniatus* were removed, after some practice, down to the P_1's inclusive if the plastochron was at a late stage, or down to the P_2's inclusive if it was at an early stage These operations were chosen because if the suggestion of Richards were correct, a removal of the P_1's should increase the angle I_1–I_2 to 90°, since normally the I_2's would have been caused to deviate from the plane at 90° to that of the I_1's by inhibitions from the P_1's Similarly, a removal of young P_2's should increase the angle P_1–I_1 to 90°, provided that young I_1's were not yet determined and the results will show that they are not determined These operations did modify the phyllotaxis, though in unexpected ways, and accordingly further experiments were made in which the leaves were removed only down to a large pair of P_2's or a pair of P_3's inclusive Also in four experiments they were removed down to a large pair of P_2's inclusive, and then one P_1 was also removed

In *Dipsacus* the P_2's from the middle of the plastochron onwards, and all the older leaves of the bud, completely enwrap the younger pairs and stem apex, so that it is not possible, as in some plants, to keep any of the older developing leaves when operating but some strong pairs of *mature* leaves were left to photosynthesize When the youngest pair removed were older than young or medium P_2's, the stem apex was not exposed and it could not be seen how many more pairs remained But the youngest pair removed was then recognized from its length, the P_2's having been found to range in length roughly from 0 25 to 0 9 mm during the plastochron The young leaves were removed under a binocular at magnification × 50 by cutting round their outer faces at the extreme base and then pressing them outwards When the operations succeeded, the extreme bases of the cut-down leaves, even of the P_1's, could still be seen directly afterwards with their outlines unbroken all round But they did not grow up, and after some days the bases of the P_1's and P_2's had disappeared In young seedlings it is difficult to get at the youngest leaves, since the whole terminal bud is sunk deep down in a tube formed by the bases of the expanded leaves But later, when in summer the seedlings are about 7 weeks old, the stem has grown and carried up the terminal bud just a little, and this was the stage at which the seedlings were operated upon They do not flower in their first year The buds were still only just above the level of the soil, and consequently the exposed stem apices and youngest leaves were very liable to be attacked by tiny mites and insects coming from the soil But a thick ring of powdered derris placed all round the exposed apical parts was found to protect them fairly well, and to be quite harmless Di-methyl-phthalate was found harmful even at a distance The exposed parts were covered thickly with cotton-wool, and the plants were left usually for about five plastochrons, which took about 18 days in a greenhouse in summer The buds were then pickled in spirit, embedded in collodion and sectioned as usual Afterwards, under a projection microscope, either the sections were drawn or the median planes of successive leaf pairs were ruled on the image with a transparent ruler, and the angles between the successive planes were measured on the drawings or rulings

4 THE MAIN EXPERIMENTS

Table 1 shows the angles between the planes of successive leaf pairs in the experiments, so far as they could be measured accurately, each angle being marked R for right (clockwise) or L for left The spaces in the table for a few of the angles contain no figures, but are marked only R or L this is because the leaves of the pairs adjoining these angles were too far from being opposite, so that the angles were not fully comparable with the others Since the bases of the removed leaves disappeared or remained only as very small fragments, the angle from the youngest pair removed to the next younger pair could not be measured Consequently, the next angle after this is the first angle recorded for each apex in the table A difficulty in calculating the means of the angles is that sometimes in the experiments the genetic spirals reversed, as will be more fully described below But another of the chief points which the table shows is that the mean angles increased, and a change in angle which goes beyond 90° and so constitutes a reversal is, in a way, a greater change and a greater increase than one which goes just to 90° Consequently, it would be misleading to calculate the means only from the values of these reversed angles measured in the new direction, in

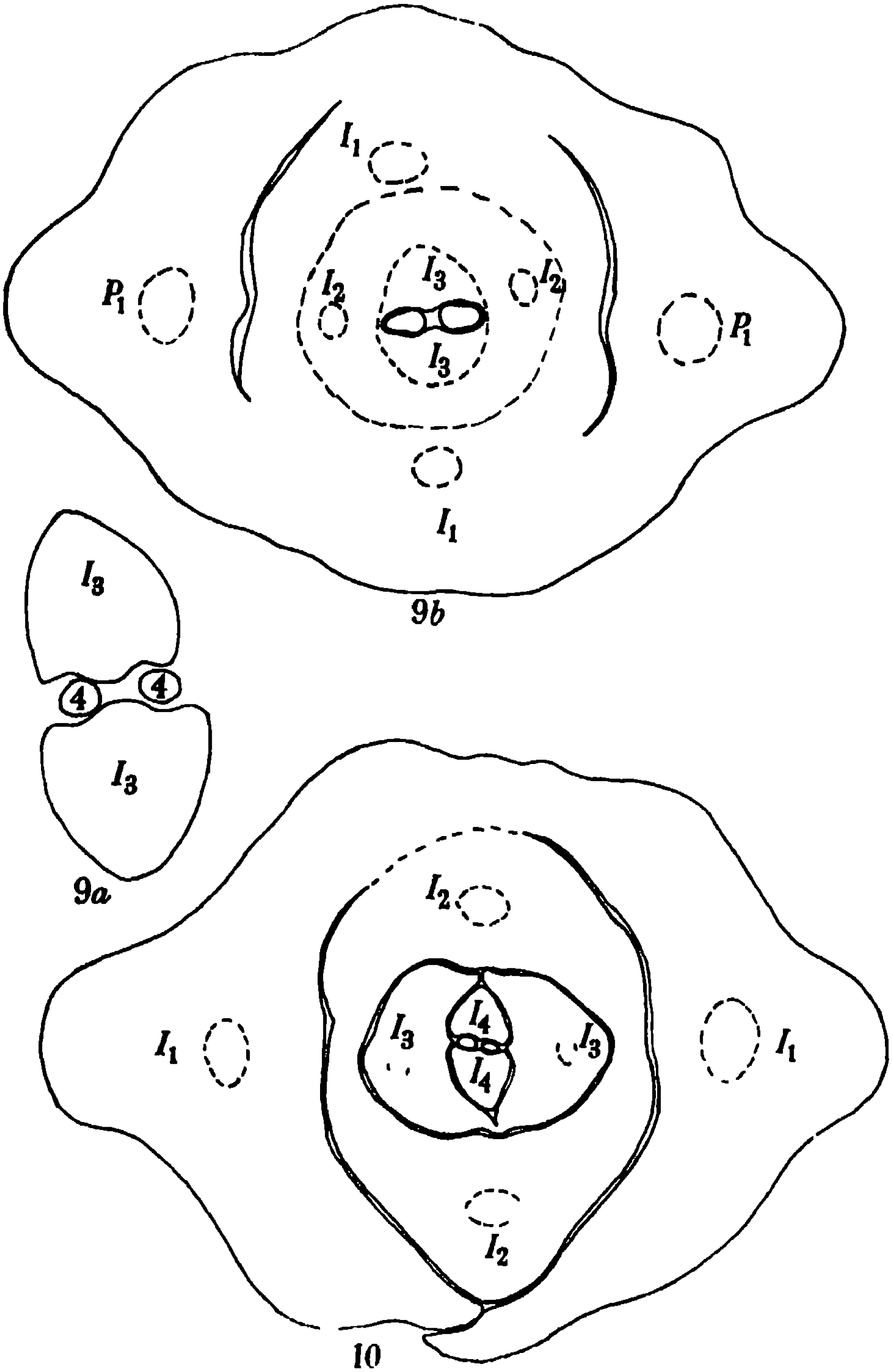


Figure 9 No 41, P_2's removed (magn *a*, × 53, *b*, × 23)

Figure 10 No 68, P_1's removed (magn × 23)

which they are less than 90° So the means marked (*a*) have been calculated from the value of each angle measured in the same direction as that of the previous angle, which gives values over 90° for the reversed angles These angles are recorded in the table, and also just below

TABLE 1 RESULTS OF EXPERIMENTS

Angles in degrees, left or right, between successive leaf pairs

Group 1, with leaves removed to P_3's inclusive nine apices

no of apex	stage of plastochron at operation	original spiral	P_2–P_1	P_1–I_1	I_1–I_2	I_2–I_3	I_3–I_4
31	early	R	70 R	81 R	78 R	82 R	
32	late	L	81 L	71 L	80 L	78 L	82 L
33	early	L	69 L	87 L	68 L		
34	middle	L	77 L	64 L	87 L	82 L	
35	late	L	64 L	75 L	72 L	90	
36	middle	R	71 R	79 R	77 R	84 R	
37	late	R	75 R	84 R	70 R	97 R 83 L	
38	very late	R	73 R	83 R	86 R		
39	early	L	78 L	67 L	85 L	77 L	87 L
		means (a)	73 1	76 8	77 8	84 3	84 5
		means (b)	73 1	76 8	77 8	82 3	84 5

Group 2, with leaves removed to P_2's inclusive twenty apices

no of apex	stage of plastochron at operation	original spiral	P_1–I_1	I_1–I_2	I_2–I_3	I_3–I_4	I_4–I_5	I_5–I_6
14	early	R	83 R	75 R	76 R	81 R		
23	very early	R	88 R	87 R	78 R	93 R 87 L	105 L 75 R	90
30	middle	L	95 L 85 R	110 R 70 L	88 L	82 L		
40	late	R	81 R	78 R	89 R	80 R		
41	middle	R	81 R	86 R	93 R 87 L	85 L		
42	late	R	76 R	83 R	87 R	81 R	83 R	
46	early	R	81 R	85 R	88 R	86 R		
47	late	R	78 R	79 R	73 R	83 R		
48	middle	R	81 R	77 R	70 R	81 R	78 R	
49	early	R	80 R	78 R	90	88 R	80 R	
51	middle	R	74 R	76 R	77 R	79 R		
52	early	R	82 R	69 R	88 R	80 R		
53	early	R	80 R	77 R	81 R	72 R	75 R	78 R
54	very early	R	79 R	88 R	65 R	93 R 87 L		
55	middle	R	80 R	78 R	88 R	77 R		
57	very early	L	82 L	76 L	79 L	87 L		
59	very early	R	100 R 80 L	86 L	78 L	88 L	80 L	
60	very early	R	79 R	88 R	77 R	90	83 R	
62	middle	L	80 L	73 L	82 L	80 L	80 L	
63	very early	L	82 L	74 L	80 L	78 L	77 L	
		means (a)	82 1	81 1	81 3	83 2	82 3	84 0
		means (b)	80 6	79 1	81 0	82 6	79 0	84 0

Group 3, with leaves removed to P_1's inclusive eleven apices

no of apex	stage of plastochron at operation	original spiral	I_1–I_2	I_2–I_3	I_3–I_4	I_4–I_5	I_5–I_6
4	late	L	86 L	75 L	82 L		
10	very late	R	83 R	80 R			
16	late	L	85 L	72 L	75 L		
17	late	L	90	— L	— R	90	79 L
19	late	L	101 L 79 R	103 R 77 L	76 L	83 L	
20	late	L	79 L	78 L	70 L	85 L	
26	middle	R	93 R 87 L	90	78 L	88 L	
50	late	L	78 L	82 L	82 L	80 L	77 L
58	late	R	90	— L	— L	— R	102 R 78 L
61	very late	L	88 L	98 L 82 R	84 R	88 R	81 R
68	late	L	91 L 89 R	86 R	93 R 87 L	79 L	
		means (a)	87 6	84 9	80 0	84 7	84 7
		means (b)	84 9	80 2	79 2	84 7	78 7

Group 4, with leaves removed to P_2's inclusive and also one P_1 removed or destroyed four apices

no of apex	stage of plastochron at operation	original spiral	P_1–I_1	I_1–I_2	I_2–I_3	I_3–I_4	I_4–I_5
24	late	R	82 R	82 R	94 R 86 L	85 L	83 L
28	late	R	78 R	87 R	77 R	85 R	78 R
29	late	L	73 L	87 L	70 L	86 L	
66	middle	L	73 L	85 L	89 L	99 L 81 R	86 R
		means (*a*)	76 5	85 2	82 5	88 7	82 3
		means (*b*)	76 5	85 2	80 5	82 2	82 3

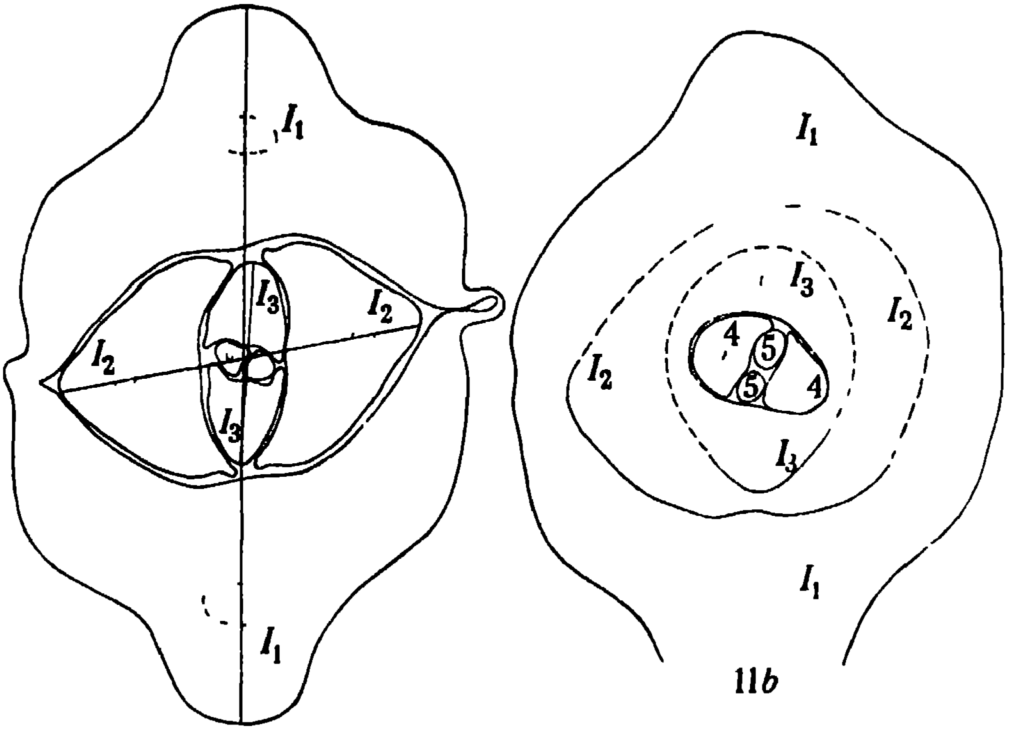
them the corresponding smaller angle measured in the new direction, which then becomes the direction for measuring the next angle, and so on Thus the pairs of values in the table serve to mark the reversals Also another set of means marked (*b*) has been calculated, for which the smaller of the paired values has been taken, though this seems less significant

Drawings of sections of several of the apical buds are shown in figures 9 to 16, the sections of each apex being labelled alphabetically from above downwards Because of the crater-like shape of the apical region, the outer leaves are often inserted higher than the inner Broken lines are used to outline the median bundles and also to outline those young leaves or parts of leaves or of the stem apex which were seen rising up from a background of tissue and not sharply cut through below The adjoining surfaces of leaves in contact are usually shown with two lines for clearness, although where the lines come close together there was regularly no chink between the leaves, which were very tightly packed in the bud

It can be seen in the table that after all the operations the mean values (*a*) of the angles recorded were considerably greater than the normal mean value of 72° 7, with S D 0 66, except of course the angle P_2–P_1 recorded after removal of the P_3's, which was already laid down and could not change The mean value of this angle, 73° 1, serves to confirm the mean of the normal angles already reported It is remarkable that the increases of angle continued even for as much as five plastochrons after the operations The increases were on the whole as might be expected, greater after removal of P_2's than P_3's, and greater still after removal of one or both P_1's But exceptions to this are the mean angle I_2–I_3 after removal of P_3's, which was as high as 84° 3 in seven apices, and the mean angle P_1–I_1, after removal of P_2's and destruction of one P_1, which was only 76° 5, but in a group of four apices only This angle P_1–I_1 was of course measured from the remaining P_1 The increases in the angles sometimes led to a phyllotaxis that was nearly decussate, for instance in figure 9, no 41, a removal of P_2's, and in figure 10, no 68, a removal of P_1's These drawings should be compared with the normal in figure 1 Figure 19, no 35, shows a single angle of 90° between the youngest two pairs of leaves, which followed rather surprisingly a removal of P_3's only

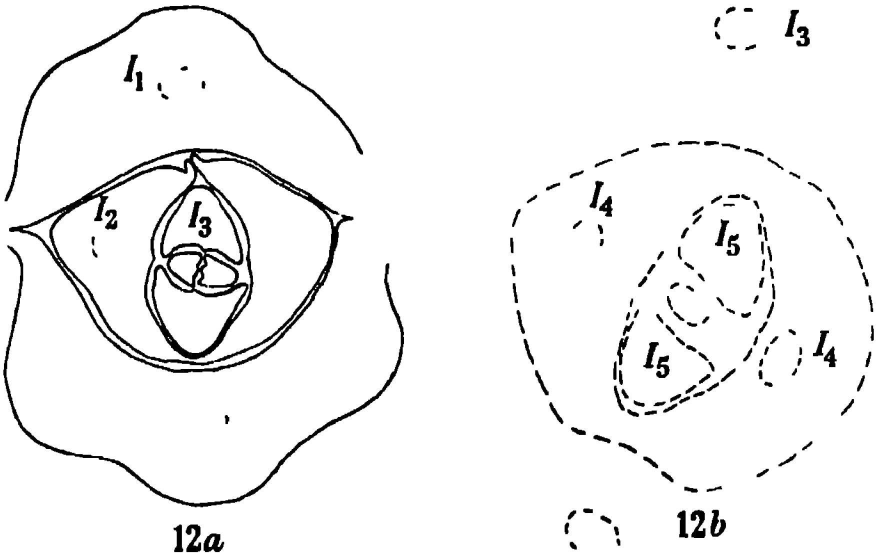
A striking reversal is illustrated in figure 11, no 19, a removal of P_1's The lines ruled through the I_1's, I_2's and I_3's make it clear that the reversal of the angle I_2–I_3 has brought back the I_3's almost exactly over the I_1's The first angle, I_1–I_2, was itself reversed from the original direction of the spiral (left), which the second reversal restores Measurements of angle can be found in the table In figure 12, no 26, also, another removal of P_1's, the angle I_1–I_2 is reversed from the original direction (right), but the spiral continues reversed In figure 13, no 23, a removal of P_2's, in which the spiral winds clockwise as far as the I_3's, there are two very late reversals, at the angles I_3–I_4 and I_4–I_5 The lines ruled through the I_2's and later pairs make this clear There are also reversals in figure 10, no 68, and in figure 16, no 66, both at the angle I_3–I_4

Altogether, amongst 177 new angles laid down after the operations, there were seventeen reversals, of which five were at the first angle recorded In the groups with one or both P_1's removed, taken alone, there were nine reversals amongst fifty-seven angles



11a

11b



12a

12b

Figure 11 No 19, P_1's removed (magn *a*, *b*, × 23)

Figure 12 No 26, P_1's removed (magn *a*, × 16, *b*, × 53)

On the upward inhibition hypothesis of Richards it was to be expected that after removal of P_1's the angle I_1–I_2 would increase to 90°, since normally the I_2's would have been caused to deviate from a position at 90° to the I_1's by inhibition from the P_1's· but the angle I_2–I_3 and subsequent angles should not be changed Similarly after removal of P_2's the angle P_1–I_1 should increase to 90°, provided that the I_1's were undetermined, but not the subsequent angles After removal of P_3's there should be no changes at all on that hypothesis

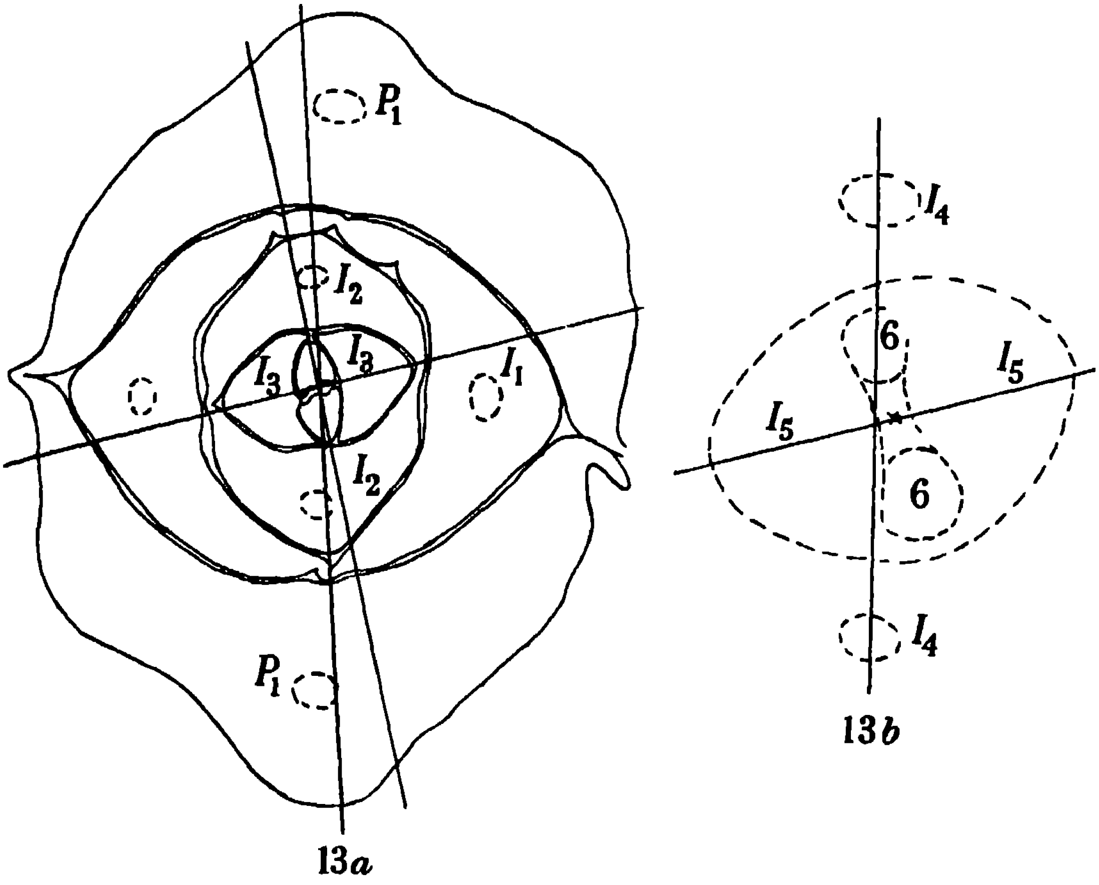
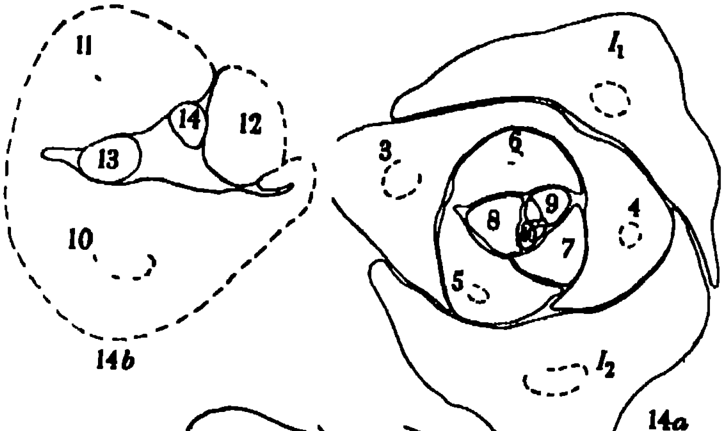


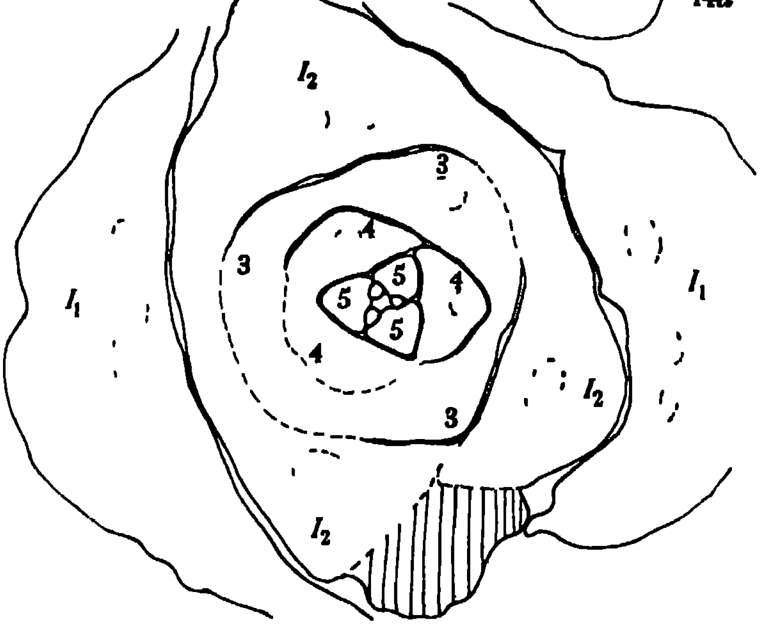
FIGURE 13 No 23, P_2's removed (magn *a*, × 19, *b*, × 60)

So the inhibition hypothesis does not account for the increases found in the angles later than I_1–I_2 after removal of P_1's, nor later than P_1–I_1 after removal of P_2's, nor for any of the increases after removal of P_3's

The reversed angles are not only unexplained on the inhibition hypothesis, but contrary to it For if the younger and older leaf pairs bordering these angles are called *n* and *n*–1, then pair *n* is situated more directly above pair *n*–2 than if it had been at right angles to pair *n*–1, although on the hypothesis pair *n*–2 inhibits pair *n* This does not indeed apply to those five of the seventeen reversed angles which were the first angles recorded, since in relation to those five angles the pair which was *n*–2 had been removed, but it does apply to the other twelve reversed angles, and in figure 11, no 19, the conflict with the inhibition hypothesis is especially striking

It should, however, be noted that throughout the experiments, although the normal tendency of the phyllotaxis to deviate continually from 90° in the same direction was much weakened, as was shown by the increases of angle and by the reversals, yet something of this tendency persisted For the mean values of the angles did not reach 90°, and the reversals were only occasional, even in the groups with one or both P_1's removed As to the time of determination of the I_1's in this species, the increases in the angle P_1–I_1 after removal of P_2's, and the big convergence of the I_1's after destruction of one P_1 in no 66, figure 16, show that certainly during the first half of the double plastochron at least, and probably for rather longer,





15

FIGURE 14 No 22, P_1's removed (magn *a*, × 11, *b*, × 40)

FIGURE 15 No 56, P_1's removed (magn × 17)

the I_1's are not determined (see table 1 for the stage of plastochron at operation) Thus the time of determination is nearly the same as in *Lupinus albus*, where we found that I_1 is probably not determined until nearly the middle of the plastochron, which is single* (Snow, M & R 1933, pp 398, 399, 1947, pp 7, 15, 1948, p 272)

* Philipson (1949, p 31) has criticized our interpretation of our experiments of undercutting presumptive areas of leaves in *Lupinus albus* (1947) on the supposed grounds that our conclusions concerning the time of determination of a leaf were based on operations that interfered with its presumptive area, so that the leaf concerned may have been determined partially, though not irreversibly But actually those conclusions, like the present, were based on operations that did *not* interfere with (that is, enter) the presumptive area of the leaf concerned, as was clearly stated (1933, p 398) Those operations were chiefly the eleven isolations of P_1 belonging to group 1 (1931, p 17, p 40 and figure 3) Also all except one of the undercut leaves (1947) were not I_1, as his statements imply, but I_2

Besides the forty-four apices included in the table there were four others that were too different to be included Two of these, in which the P_1's were removed or one P_1 was destroyed, had leaves irregularly paired, one, figure 14, no 22, in which the P_1's were removed when of medium size, became spiral, and one, figure 15, no 56, in which the P_1's were removed when large, formed whorls of three after the I_1's The factor leading to the spiral shown in figure 14 cannot be discovered, but may have been some slight accidental injury The operation itself would not be expected to lead to a spiral, though a diagonal split of the stem apex would be likely to do so, as in decussates

But the development of the three-whorled apex shown in figure 15 can probably be explained as follows When this apex was examined 7 days after the operation, the I_1's appeared to be wilted and irregular in shape, as they still are in the drawing, presumably because the covering of cotton-wool had not been close enough In the drawing it can be seen also that the two I_2's which are closest together are joined by some unorganized tissue which is shown cross-hatched It therefore seems probable that an original I_2 collapsed in the period of wilting, and two new I_2's were then formed from its base, making a whorl of 3 The divided bundle of the other I_2 suggests that it nearly did the same It may be noted that after the I_2's the leaves of alternate whorls are almost exactly superposed

Since in the main experiments the increases of the angles between leaf-pairs continued for several plastochrons after the operations and were not in any very obvious way junctional consequences of the operations, it was thought that they might be due to some persisting physiological change in the conditions of growth, and accordingly some attempts were made to change these conditions in other ways In two apices, nos 62 and 63 of the table, the P_2's were removed in the usual way, but then much more light than usual was admitted, with due precautions, to the stem apex and youngest leaves But the subsequent changes of angles in these two were not in any way exceptional

More effective was the inverse stimulation by gravity of two plants These plants were not operated upon, but the pots containing them were propped in the inverse position with a sheet of white paper below them as reflector The older leaves were also partly lit from above, since they projected beyond the pot The apical buds were much retarded in growth by the inversion, and after 16 days they had nearly stopped growing Then the pots were turned upright, the apical buds began slowly to grow again, and after a further period of about 25 days they were pickled At the start of the inversion an outer pair of leaves of the bud had been marked and measured, and by calculating from the length of this marked pair, it was estimated which had been the youngest pair at that time From that pair onwards the angles between successive pairs were measured on drawings or rulings of bud sections down to the youngest pair finally visible in no 1 and the youngest but one in no 2, and the following values in degrees were recorded

In no 1	72	67	69	69	72	69	—
In no 2	72	66	68	64	63	64	70

There can be little doubt that the inversion had *decreased* the angles below the normal mean of 72° 7, especially as the first angles recorded were probably laid down before the inversion had produced its full effect These two apices will be further discussed below

5 Further observations and suggested explanations

The evidence of the experiments reported is decidedly against the explanation of bijugy which they were designed to test, and it therefore needs to be considered whether the bijugy of *Dipsacus* can be explained in some other way which is consistent with the experiments It must first be pointed out that there is evidence of an active whorl-forming process in *Dipsacus*, similar to that which the writer found in decussate apices of Labiatae (1942), and which he showed to comprise one factor for equalizing the levels of the positions in which leaves are formed, and another factor for equalizing the lateral spacing of these positions For the equalizing of levels in *Dipsacus* is shown strikingly in figure 16, no 66, in which the I_1's converged strongly (29°) towards the position of a destroyed P_1, but the I_2's arose very accurately at the same level, though junctional factors alone would have caused the I_2 in the larger angle to arise earlier and lower The equalizing of lateral spacing is shown in the three-whorled apex, figure 15, no 56, in which the leaves of the first whorl of three are spaced very unequally, but those of the later whorls fairly equally Several other examples of the whorl-forming tendency were found in *Dipsacus*, although the experiments were not designed to test for this tendency, as were those on the Labiatae Incidentally it may be noted that the whorl-forming tendency in the plants of these families

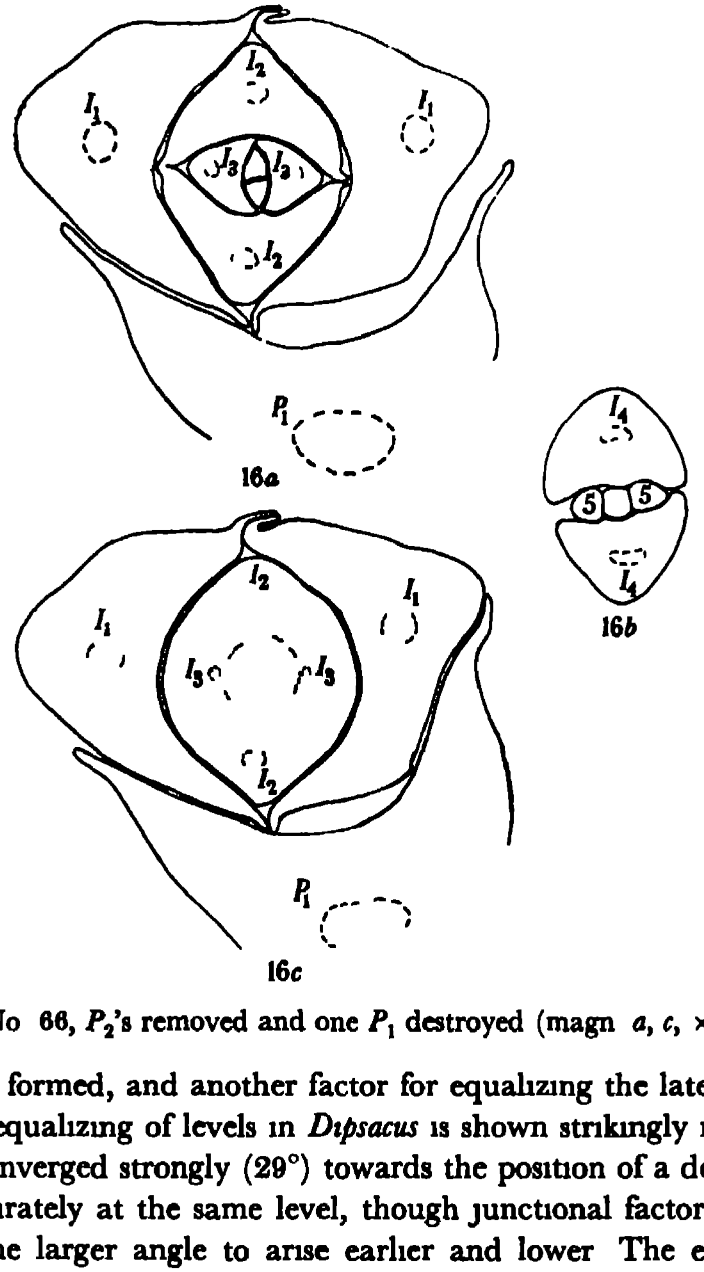
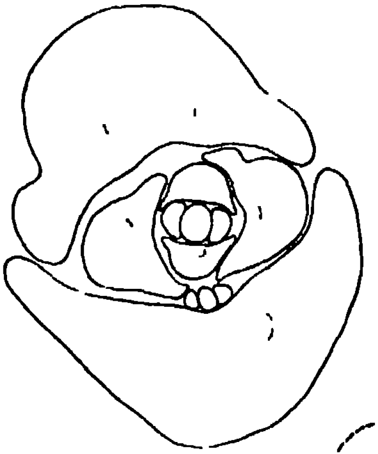


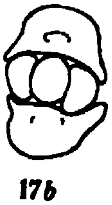
FIGURE 16 No 66, P_2's removed and one P_1 destroyed (magn *a*, *c*, × 12, *b*, × 40)

is *not* a tendency to form leaves in pairs, since it acts similarly on groups of three or more leaves, if the junctional factors alone would have caused those leaves to arise nearly in a whorl The fact that normally in these plants the vegetative whorls contain two leaves can be explained on junctional grounds These matters and the experimental production of spirals in decussate species were discussed more fully before (Snow 1942)

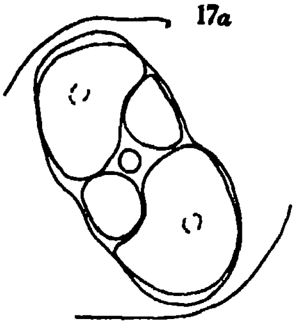
The formation of whorls, therefore, in *Dipsacus* and in the decussates is an active and primary process of some kind and is not merely a geometric consequence of the even numbers of the parastichies, as Church maintained (1904) Accordingly the problem of the bijugy of *Dipsacus* is how it is that the angles between successive leaf pairs deviate constantly from 90° One factor that may play a part in bringing this about is suggested by comparison with seedlings of an exceptional labiate, *Salvia horminoides*, which form close and clearly bijugate rosettes Two drawings of a favourable section through the apex of a rosette are shown in figure 17*a*, *b*, at different magnifications The plastochron is at a late stage, the stem apex is elliptic, and the next pair of leaves is being or has been determined on the narrow ends of the ellipse So it is clear that each leaf of this next pair will make contacts 1, 1 and 2—that is to say that it will make contact at its base not only with the leaves of the next older pair (contacts 1 and 1), as do the youngest leaves of straight decussate apices, but also with a leaf of the second older pair (contact 2) The making of contact 2 is naturally due to the smaller arc covered by each leaf



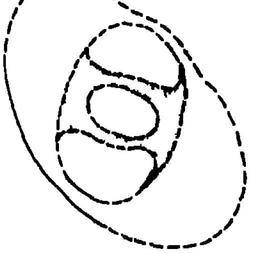
17*a*



17*b*



18*a*



18*b*

FIGURE 17 *Salvia horminoides*, normal apex (magn *a*, × 38, *b*, × 54)

FIGURE 18 *Dipsacus laciniatus*, apex of an inverted plant (magn *a*, *b*, × 40)

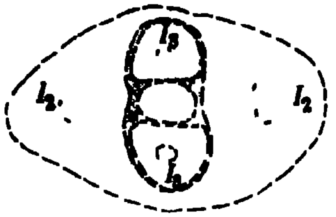
It can therefore readily be understood on the basis of a junctional and space-filling theory of leaf determination that the phyllotaxis of these rosettes deviates from straight decussation

Indeed the change is quite similar to the transition common in other seedlings from distichy to a spiral with contacts 1 and 2, which is due to a fall in leaf arc and is well described by van Iterson (1907) The explanation of the change is clear if one considers the boundary line formed by the upper margins of the bases of the young leaves round the stem apex Thus in figure 17 of *S hormınoides*, since the parts of the stem apex from which the new pair of leaves will arise make contact with the leaves of pair 2, the position which is the lowest for each new leaf, and which therefore will first become available for it, is not directly over the centre of leaf 2, where the circular base of that leaf comes nearest to the growing-point, but a little to one side, in one of the corners between leaf 2 and a leaf of pair 1 Accordingly the new leaf deviates a little to one side, and the equal spacing factor of the whorl-forming process ensures that the other leaf of the new pair deviates in the same sense It is also clear enough that the deviations of successive pairs will continue in the same sense

In *Dipsacus*, on the other hand, it seems at first that the deviations of the leaf-pairs from straight decussation cannot be explained in a similar way, since each new leaf makes contact only with the next older pair But then the shapes of the leaf bases are very peculiar and far from being simply circular, since the bases of each pair unite by a low rim before the end of their first plastochron, as was described in § 2, figures 2 and 3 Moreover in observations of the *Dipsacus* apices from which pairs of large P_1's were removed, it often appeared that the boundary formed round the stem-apex by the bases of these P_1's with their united rims was far from being circular or elliptic, but distinctly showed four sides and four corners So it seems quite possible that the united rims act as another pair of contacts, and that the positions which normally first become available for the next pair of leaves, if their arcs are small enough, are nearly the corner positions, as in *Salvia horminoides*, and not the median positions at right angles to the previous pair

On this basis an explanation can be suggested for the increases of the angles after the operations, though something more is needed to explain the occasional reversals For it is quite possible that when the leaves of the buds were all, or nearly all, removed, the arcs of the leaves formed subsequently were slightly larger than the normal, and that in the inverted plants they were slightly smaller than the normal The increase of arc would then increase the angles between the leaf-pairs by preventing the new leaves from fitting so closely into the corner positions, whereas the decreases of arc would decrease these angles by enabling the new leaves to fit more closely into those positions There are indeed some indications that the leaf arcs were larger after the operations and smaller after the inversions Thus figure 19 is of a favourable section through the stem apex of no 35, one of the plants operated upon It shows a stage slightly after mid-plastochron, and one can see that the arcs of the youngest pair of leaves, which are the I_3's, are already so large that they could not easily be fitted into corner positions between the next older pair and their united rims This section was lucky, since the angle had just risen to 90° (see the table)

Figure 20, no 41, is at a rather later stage of the plastochron, and only the inner contour line of the second pair, which were the I_3's, is shown, since the section was below their outer insertions It can be seen again that the youngest pair is too large to occupy corner positions The angle I_3–I_4 was 85° left Figure 21, no 47, shows an apical section made at the very end of a plastochron, when the youngest pair had already united The stippled area within the contour lines of the youngest pair is all apical tissue, and appears markedly four-sided The central ellipse is a small apical dome rising up from this background Figure 22, no 42, shows an earlier stage at about mid-plastochron Here it looks as if the bases of the youngest pair, which are the I_5's, could have deviated further into the corner positions, but they may not yet have grown to occupy the whole of the area over which they were determined, which is the critical area on a space-filling theory The angle I_4–I_5 in this apex was measured from other sections as 83° R



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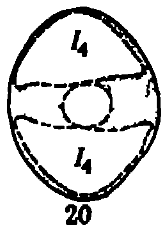

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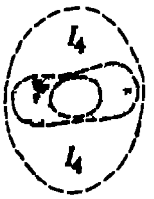

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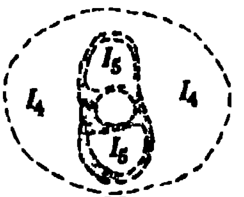

22

FIGURE 19 No 35, P_3's removed (magn ×54)

FIGURE 20 No 41, P_2's removed (magn ×40)

FIGURE 21 No 47, P_2's removed (magn ×40)

FIGURE 22 No 42, P_2's removed (magn ×40)

A great contrast with these apices and with others of the plants operated upon was provided by the apices of the two inverted plants with small angles Two consecutive sections of the first of these are shown in figures 18*a*, *b* The higher section, figure 18*a*, has just cut the tip of the apical dome, and has cut the youngest pair just above their insertions Judging from this section alone, one would have thought that the contacts of the bases of the youngest pair were 1, 1 and 2, as in *S horminoides*, but the next lower section shows that the second pair are united by rims, and that each leaf of the youngest pair makes contact at its base with the next older pair, and with their united rims only, and that it fits very closely into one of the corner positions of the boundary line So in this apex it does seem that the united rims of the 2's have acted as contact members in the same way as the 3's in *S horminoides* (contact 2), and this forms a strong piece of evidence in favour of the explanation of the normal bijugy as due to a contact of the 1's with the united rims of the 2's But many more observations are needed to discover how generally this factor may be at work

Another factor which may play a part in causing the normal bijugy of *Dipsacus* is pressure exerted by the upper parts of the second pair of leaves (the P_2's of the operations) on the sides of the stem apex, which they touch in the way described in § 2 For there is evidence from the experiments of Němec (1903) that pressure on part of a stem apex tends to inhibit the formation of a leaf by that part, as might indeed be expected This factor may act together with the factor due to the spatial relations of the leaf bases already discussed in causing the bijugy, since the two factors are quite compatible It should not be confused with Schwendener's hypothesis of a shifting of *existing* young leaves by lateral pressures between them The contact of the upper parts of the P_2's with the stem apex was found to persist through the first half of the plastochron, or a little longer, and this is the right time for influencing the positions of the pair about to arise (the I_1's of the operations), since the evidence showed that the I_1's were not determined until soon after mid-plastochron It can be understood that the pressure of the P_2's, by tending to inhibit the formation of leaves on the parts of the apex directly above them, would cause the I_1's to deviate a little from the plane at right angles to the P_1's, and so to deviate from straight decussation

This is exactly the way in which physiological upward inhibitions are supposed by Richards to act, and it might therefore be thought that the explanation based on pressure from the P_2's must fail to explain the long continuing increases of angle after the operations in just the same way as does the hypothesis of Richards But this is not so, since the pressure exerted by the P_2's on the apex may depend on the pressure which they themselves receive from the older leaves outside them Consequently, when in the operations these outer leaves, and usually the P_2's themselves, were removed, the pressures exerted afterwards on the apex by the successive pairs, as each became in its turn the second oldest pair, may have been less, and this would explain the long continuing increases of angle, and the increases after removal of the P_3's only

This suggestion is supported by the following observation When the outer leaves were removed, the P_2's were regularly found pressed tightly together along their inner surfaces, and then sometimes the buds were covered up and left for a few hours because bleeding from various cut surfaces made it difficult to see When the buds were uncovered again, the P_2's were often found to be no longer pressed so tightly together, so that presumably they were not pressing so hard on the stem apex either

But the reversals of angle in the experiments can be explained neither on the basis of the spatial relations of the leaf-bases alone, as was pointed out above, nor on the basis of the pressure from the P_2's alone For if the latter were the only factor causing the normal deviations from decussation, then it would be expected that when this pressure was diminished or abolished, the angles would increase up to 90°, but not reverse The reversals can, however, be explained in terms of both these factors working together, and it seems worth while to set out this explanation briefly, in order that it may not seem that both these factors are disproved because the reversals cannot be explained on the basis of either factor alone

The explanation can readily be understood if one starts from a comparison with *Salvia horminoides*, with its contacts 1, 1 and 2 (figure 17) In that species, as was pointed out, the angles deviate from 90° because in each new pair of leaves, which will be called n, each leaf arises in a corner position of the boundary line, between a leaf of pair $n-1$ and another of pair $n-2$ Further, when once the deviations have started, pair $n-1$ is not at right angles to pair $n-2$, and consequently, of the two corner positions in which each leaf n might arise, one is wider than the other So leaf *n* arises in the wider gap, and thereby the sense of the deviation from 90° is kept constant

In *Dipsacus* it was suggested that the contacts of pair *n* with the united rims of pair *n*–1 act similarly to the contacts with pair *n*–2 in *Salvia horminoides*, and so cause the angles to deviate from 90° But the boundary line formed by the united rims in *Dipsacus* does not rise up in the middle towards the summit of the apex nearly so much, if at all, as does the boundary line formed by pair *n*–2 in *Salvia horminoides* Consequently, the two corner positions in which leaf *n* might arise are not so sharply differentiated into a wider and a narrower space, though they may differ slightly, and so far as this factor alone is concerned the sense of the deviation is not likely to be kept so firmly constant But if normally in *Dipsacus* the pressure from the upper parts of pair *n*–2 (the P_2's) on the stem apex also plays a part in making the angles deviate from 90°, this factor will help to keep the sense of the deviation constant For when the deviations have started, the greatest pressure from each successive pair *n*–2 will come on the apex a little towards one constant side of the plane at right angles to the plane of pair *n*–1 Consequently, when in the operations the pressure from each pair *n*–2 is abolished or diminished, this factor will no longer be at work, and the new pairs of leaves may arise in those corner positions in which they do not normally arise, thereby reversing the angles

However these suggested explanations are far from being firmly established, and many more observations are needed to establish how generally either or both of the factors suggested may be at work in causing bijugy In particular it needs to be observed whether in the other Dipsacaceae there are similar united leaf rims, and whether the P_2's touch the stem apex similarly In *Scabiosa caucasica* the writer has found the rims of the youngest pair almost united near the end of a plastochron

It was pointed out that bijugy is caused by another factor in *Salvia horminoides*, and it remains possible that in species of some other families bijugy may be caused by upward physiological inhibitions, as suggested by Richards, though in *Dipsacus* the evidence is against this In any case, the factor already mentioned which equalizes the spacing of the members of a whorl may be a physiological inhibition or repulsion of some kind, but one that acts only between leaves that are about to arise at the same level, or very nearly so

The idea that several factors may cause bijugy, and that sometimes two such factors may act together in the same plant, need not seem surprising, since bijugy in rosette plants has a clear functional value So it is quite probable that natural selection may have worked up several different ways of bringing it about

I am indebted to my wife for help in finding out how to operate on *Dipsacus*, and for a valuable discussion of the interpretation

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A CONTRIBUTION TO THE STUDY OF THE EOCENE IN WESTERN PAKISTAN AND WESTERN INDIA

B THE DESCRIPTION OF THE LAMELLIBRANCHIA FROM STANDARD SECTIONS IN THE RAKHI NALA AND ZINDA PIR AREAS OF THE WESTERN PUNJAB AND IN THE KOHAT DISTRICT

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(*Communicated by A E Trueman, F R S—Received* 24 *April* 1950—
Revised 2 *August* 1950)

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The Lamellibranchia here recorded or described comprise 147 forms, 135 of which have received specific names Of the forty-four previously named species, four had not been recorded from Pakistan or India before Largely owing to the nature of some of the beds from which collections were made, eighty-nine of the species described are new Two new genera and four new subgenera are proposed, and also one new generic name to replace a pre-employed name

The fauna recorded, together with the Gastropoda to be described subsequently, forms part of the material constituting the basis for the consideration of the classification and correlation of the Eocene of Western Pakistan and western India, which the writer has published elsewhere

INTRODUCTION

In this paper are described the Lamellibranchia collected from standard sections in the Eocene of the Rakhi Nala and Zinda Pir areas of the western Punjab and of the Kohat District The writer has described the geology of the standard sections (1950*c*), in which paper will be found full details of the geological successions, copies of the complete faunal lists and details of the stratigraphical horizons of all fossil beds have been deposited in the library of the Geological Society for reference

The classification here adopted is a compromise of those of Dr A M Davies (1935) and Thiele (1929–31, 1934) All specimens for which registered numbers are given have been deposited in the Geological Department of the British Museum of Natural History The Scaphopoda and Gastropoda will be described in a subsequent paper

Text In the description of species, it should be assumed that internal shell characters have been described only where the material has permitted Under the headings 'Material', the italic numbers following the fossil bed numbers refer to the number of individuals collected

Acknowledgements The writer is greatly indebted to Dr L R Cox for assistance and advice which he has unstintingly given at all stages of the work, to the librarians in the British Museum of Natural History, South Kensington, for assistance in searching for references, to Mr W N Edwards, Keeper of the Geological Department of the British Museum of Natural History, for arranging for facilities to undertake the work there, and to the Directors of the Attock Oil Co Ltd and the Burmah Oil Co Ltd for grants towards the cost of publication The wash drawings from which the illustrations were prepared were made by Mr D E Woodall, A R C A, and the writer is indebted to the Directors of the Burmah Oil Co Ltd for defraying the expense thereof

LAMELLIBRANCHIA

Order PROTOBRANCHIA

Superfamily NUCULACEA

Family NUCULIDAE

Genus *NUCULA* Lamarck, 1799

(*Mém Soc Hist nat Paris*, p 97)

TYPE SPECIES *Arca nucleus* Linné, Recent, monotypy

NUCULA DOMANDAENSIS n sp

(Figures 1*a*, *b*, plate 9)

MATERIAL Top of Eocene the holotype (Reg No L 77877) and 7 topotypes (Reg No L 77878–83) from 4 miles north of Domanda, Dera Ismail Khan District, North-West Frontier Province *Rakhi Nala section* Upper Chocolate Clays (upper part, local zone 13) (FB F 1996, *1*, FB F 1986, *12*, Reg No L 79786–92), *Pellatispira* Beds (local zone 15) (FB F 1993, *2*), *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2541, *2*, FB F 2540, *1*, FB F 2539, *2*), Upper Chocolate Clays (upper part, local zone 13) (FB F 2520, *2*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2517, *1*)

DESCRIPTION Shell of only moderate size, subtriangular in outline, not very strongly inflated Umbos distinct and rather pointed, situated posterior to the median line at about three-thirteenths of the length Antero-dorsal margin rather long, slightly convex, moderately descendent Anterior end moderately sharply rounded Ventral margin rather convex, its posterior margin more steeply rising than its anterior end Posterior end bluntly pointed where it joins the postero-dorsal margin which is steeply descendent and straight as a whole, but with a slight, gentle median convexity corresponding to the slightly convex central portion of the escutcheon When well preserved the surface is smooth, but there is a radial shell structure which shows as fine, dark-coloured radial lines When the surface of the shell becomes worn, these radial lines are more resistant and stand up as fine radial ridges, they number 60 on the holotype between the margins of the escutcheon and lunule Valve margins strongly crenulated internally, with crenulations corresponding to the intervals between the dark-coloured radial lines Lunule long and lanceolate, not well defined on its outer margins where it merges with the lateral surface of the shell in a very obtuse angle, each part slightly convex and ornamented with transverse ridges There are indications of about 23 of these ridges on the holotype, placed almost at right angles or slightly antecurrent to the antero-dorsal margin of the shell, becoming finer and still more antecurrent near the outer edge of the lunule, and often somewhat bent Escutcheon rather broad and slightly convex, rather sunken as a whole but with the central area slightly convex, limited by a sharp raised ridge at its junction with the lateral margin of the shell Holotype with 15 transverse, raised ridges on the escutcheon, they are slightly concave towards the umbos and do not quite reach the limiting raised ridge Fine concentric granular threads tend to be present on the lunule and escutcheon and closely adjacent areas of the lateral surfaces Some specimens are a little more elongate than the holotype

Dimensions Holotype length 12 9 mm , height 10 4 mm , thickness (both valves) 5 8 mm

Remarks The holotype has been selected from a series of better preserved specimens collected by Mr Pinfold, rather than from the standard section collections Mr Pinfold's specimens came from the top of the Eocene near Domanda, and our knowledge of the area indicates that they are from the *Pellatispira* Beds (local zone 15)

Nucula alcocki Noetling (1895, p 8, Pl 1, figs 5–7), from the Oligocene and Miocene of Burma, is a little larger (length 17 0 mm), a little more elongate, has a slightly different outline, and does not possess the distinctive raised ornament on the lunule and escutcheon The type of *N baboensis* J de C Sowerby (1839, p 328, Pl 24, fig 5), from the Khirthar of Baboa Hill, Cutch, is an internal mould showing no traces of crenulations on the valve margins, so that it may be a *Leionucula*, it is distinctly larger (length 25 4 mm), and has a slightly shorter and less steeply sloping postero-dorsal margin and rather less conspicuous umbos *N hizensis* Nagao (1928, p 19(9), Pl 7, figs 11–16, 18), from the Okinoshima Beds and Iojima Beds of Japan, has a distinctly more convex ventral margin *N aralensis* Dukooizen, from the Eocene of the area between the Aral Sea and Lake Chalkar (1924, p 35, Pl 1, fig 8), has a much finer radial shell structure and a more angular outline (see also Lukovitch, 1926, p 44, Pl 2, fig 8) *N kasakstanica* Ruzin (1935, p 41, Pl 1, fig 3), from the Aral Sea Palaeogene, has less elevated umbos and a less convex ventral margin Although *N bowerbankii* J de C Sowerby, from the London Clay of England and the Eocene of the northern Alps, Belgium and Turkestan, has the same outline, radial structure and crenulated valve margins, it is larger, more inflated, and entirely lacks the raised ornament on the lunule and escutcheon *N rugulosa* von Koenen (1893, p 1115, Pl 73, figs 19–23), from the Lower Oligocene of north Germany, is similar in size and outline but is a little more inflated, has a more convex ventral margin and has no raised ornament on the lunule and escutcheon *N consors* Wood (1864, p 111, Pl 19, figs 7*a*,*b*), from the Eocene of Highgate, has slightly less prominent umbos and the escutcheon is much more sunken and smooth *N sericea* Wood (1864, p 119, Pl 19, fig 3), from the Eocene of White Cliff and Huntingbridge, does not have quite such high umbos, has feeble concentric ornament and a smooth escutcheon *N submargaritacea* Rouault (1850, p 469, Pl 14, fig 20), from the Eocene of Bos d'Arros, is not so high *N similis* Sowerby as figured by Cossmann (1887, Pl 5, figs 23, 24), from the Eocene of Le Ruel, has the umbos even more posteriorly situated

Subgenus *LAMELLINUCULA* Schenck, 1944

(*J Paleont* **18**, no 1, p 97, fig 1)

Type species *Nucula tamatavica* Odhner, Recent, original designation

NUCULA (*LAMELLINUCULA*) *PAKISTANICA* n sp

(Figures 2*a*,*b*, plate 9)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) FB F 2571, *1*, FB F 2564, the holotype, Reg No L 79793, and 5 topotypes, Reg No L 79794–8, FB F 2562, *1*, FB F 2561, *2*)

Description Small, obliquely subtriangular in outline, moderately strongly inflated, especially umbonally Prodissoconch small, apparently smooth Umbos rather high, moderately pointed, situated posterior to the median line at about five-sixths of the length Antero-dorsal margin rather long, straight or very slightly convex, moderately steeply descendent Anterior end narrowly rounded Ventral margin moderately convex Posterior end broadly rounded Postero-dorsal margin slightly convex, steeply descendent Shell ornamented with fine, sharp, distinct, concentric threads which are, at most, only one-half the width of their intervals and are minutely frilled There are 19 or 20 such threads on the holotype, spaced about 11 to the mm ventrally Valve margins finely crenulated ventrally Lunule and escutcheon not well preserved. Lunule apparently not very elongate, only slightly sunk, smooth Escutcheon cordiform, wide, not sunk Compression tends to make young specimens less inflated, and weathering makes the concentric threads appear finer and more widely spaced

Dimensions Holotype length 2 3 mm , height 1 9 mm , thickness (both valves) 1 3 mm

Remarks Closely related to *Nucula minor* Deshayes as figured by Wood (1864, p 114, Pl 18, fig 10) and Cossmann & Pissarro (1904*a*, Pl 33, fig 104–12), from the Eocene of Bracklesham and the Lutetian and Bartonian of France, but more triangular, and with a more pointed anterior end and less convex antero-ventral margin It differs similarly from *N fragilis* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 33, fig 104–9), from the Cuisian of France It is smaller, with less distinct radial ornament, with a less distinct escutcheon and a more pointed anterior end compared with *N nystana* Le Hon as figured by Glibert (1936, p 13, fig 7, Pl 1, fig 3), from the Wemmel Sands (Bartonian) of Belgium The antero-dorsal margin is straighter and the shell is smaller and does not display the delicate radial ornament of *N regnorum* Wrigley (1929*a*, p 52, fig 6), from the

London Clay of Bognor It is even more triangular, with a more pointed umbo, a straighter antero-dorsal margin, and more distinct ornament than *N capillacea* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 33, fig 104–11), from the Lutetian of the Paris Basin

The form and ornament place this species as a *Lamellinucula* rather than as a *Nucula, sensu stricto* Schenck himself states that *N regnorum* may be a *Lamellinucula*

NUCULA (*LAMELLINUCULA*) *COSTACALLISTIFORMIS* n sp

(Figures 3*a*, *b*, plate 9)

Material *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 79799, and 8 topotypes, 7 of which are immature, Reg No L 79800–5)

Description Shell small, suboval, having the form of a small *Costacallista*, moderately inflated Prodissoconch not distinctly seen, apparently moderately large and smooth, this appearance may, however, be due to wear of the umbonal region Young forms tend to be less transverse Umbos not large, not prominent, situated posterior to the median line at about five-seventeenths of the length Antero-dorsal margin moderately long, slightly convex, gently descendent Anterior end rather narrowly rounded Ventral margin distinctly convex Posterior end broadly rounded with a slight indication of angularity Postero-dorsal margin almost straight, slightly convex, moderately short, rather steeply descendent Ornament consisting of distinct concentric threads or fine lamellae of about the same width as or slightly wider than their intervals, there are about 19 of them on the holotype between the ventral margin and the smooth umbonal region, and about 10 to the mm ventrally Internal ventral margin of valves finely crenulated Using high magnification the concentric lamellae appear to be vaguely frilled ventrally, and a very fine radial shell structure is seen Lunule not well preserved, long and lanceolate, with the hinge teeth showing through Escutcheon similarly ill-preserved, appearing rather small and cordiform

Dimensions Holotype length 2 55 mm , height 1 9 mm , thickness (both valves) 1 35 mm

Remarks This species is not so high as and is less triangular than *Nucula* (*Lamellinucula*) *pakistanica* It is smaller, more oval, and lacks the concave postero-dorsal outline of *N chasteli* Nyst as figured by Zinndorf (1928, p 40, Pl 4, figs 8–13), from the Rupelian of Offenbach, Germany *N capillacea* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 33, fig 104–11), from the Lutetian of Grignon, is less callistiform in outline, more pointed posteriorly, and has higher umbos and rather less distinct concentric ornament

NUCULA (*LAMELLINUCULA*) *DEPRESSILUNULATA* n sp

(Figures 4*a*, *b*, plate 9, figure 28, plate 10)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB. F 2539, the holotype, Reg No L 79806, and 2 topotypes, Reg No L 79807–8, FB F 2538, *1*)

Description Shell oval-subtriangular in outline, of moderate size, only moderately inflated Umbos moderately high and pointed, situated posterior to the median line at about one-third of the length Antero-dorsal margin distinctly arched, almost horizontal near the umbo, becoming quite steeply descendent near the anterior end which is rather narrowly rounded Ventral margin moderately convex Posterior end and postero-dorsal margin not preserved intact, the posterior end, however, does not appear to have been sharply angular Ornament consisting of strong concentric threads or lamellae which are microscopically frilled, these lamellae are of about the same width as their intervals in the later stages of growth, but narrower than their intervals in the umbonal region, there are about 18 in 7 5 mm on the ventral portion of the holotype There is also a microscopic radial shell structure Lunule long and broadly lanceolate, quite smooth, and deeply sunk with reference to the antero-dorsal termination of the ornamented part of the shell, the effect is rather that of an oblique lucinoid fold, and the anterior ornamented portion of the shell is distinctly more narrowly rounded than the actual outline of the margin Traces of nuculiform hinge teeth can be determined on the holotype

Dimensions Holotype length (incomplete) 17 7 mm , height (restored) 17 5 mm , thickness not determinable, ratio of length to height based on concentric lamellae on the later part of the shell, 3 2

Remarks Although all specimens are fragmentary, the form, ornament and characters of the lunule enable the species to be recognized easily *Nucula archiaci* Cossmann & Pissarro (1927, p 14, Pl 2, figs 24–26), from the uppermost Ranikot of Jherruck, is rather similar in outline, but has slightly finer ornament, and lacks the above-described type of lunule

NUCULA (*LAMELLINUCULA*) *SORIENSIS* n sp

(Figures 5*a*, *b*, *c*, plate 9)

Material *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 79811, and 4 crushed topotypes, Reg No L 79812–5)

Description Shell small, outline oval, wider than high Umbos not prominent, moderately broadly rounded Shell only moderately inflated when not crushed Umbos situated posterior to the median line at about one-third of the length Judging from the ornament, the posterior end was a little more broadly rounded than the anterior, and the ventral margin was distinctly convex Ornament consisting of fine concentric lamellae which are very vaguely frilled and slightly wider than their intervals, there are 9 or 10 lamellae between points 1 0 and 2 0 mm distant vertically from the umbo There is an extremely fine radial shell structure It cannot be seen whether or not the valve margins were internally crenulated ventrally, but they probably were Lunule elongate, ill-defined, with at least 13 short transverse raised ridges Escutcheon not well seen, obscured by matrix on the holotype The holotype shows part of the hinge, which is broken at both ends, there are at least 6 taxodont teeth posterior to the umbo and 13 anterior to it

Dimensions Holotype length (incomplete) 2 85 mm , height (incomplete) 1 9 mm , thickness (measured along plane of commissure) 1 3 mm , ratio of length to height calculated from one of the concentric lamellae, 30 23

Remarks None of the specimens is complete, but the ornament is well preserved, the outline can be determined, and part of the hinge is seen The form and ornament appear to be characteristic The species is placed in the subgenus *Lamellinucula* on account of the nature of the ornament

Subgenus *GIBBONUCULA* n subg

Type species *Nucula* (*Gibbonucula*) *corbuliformis* n sp , Lower Eocene

Subgeneric characters Small, corbuliform, strongly inflated Lunule and escutcheon poorly defined Thick-shelled for the size, with vaguely frilled concentric lamellae, and a very fine radial shell structure, valve margins internally distinctly crenulated ventrally Hinge not well seen, with five taxodont teeth posterior to the umbo and at least seven anterior to the umbo

This subgenus seems to be quite distinct from any of the nuculid forms considered by Schenck (1934, 1939, 1944), the form and ornament are quite different from the subgenus *Lamellinucula* Schenck (1944)

NUCULA (*GIBBONUCULA*) *CORBULIFORMIS* n sp

(Figures 6*a*, *b*, *c*, plate 9)

Material *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2677, 2, Reg No L 79823–4, FB F 2678, the holotype, Reg No L 79816, and 6 topotypes, Reg No L 79817–22)

Description Shell small, corbuliform, equivalve, very stongly inflated, thick-shelled for the size Outline oval-subtriangular Umbos prominent, strongly incurved and moderately opisthogyrous, situated a little posterior to the median line at about five-eighths of the length Antero-dorsal margin slightly convex, of moderate length, rather steeply descendent Anterior end rather narrowly rounded Ventral margin strongly convex Posterior end bluntly angular Postero-dorsal margin slightly concave, moderately long, rather steeply descendent Ornament consisting of vaguely frilled, strong, concentric threads or fine lamellae of approximately the same width as their intervals, they tend to be more widely spaced in the young stages, and a little more closely spaced near the ventral margin in adults, there are about 19 on the holotype Prodissoconch evidently very small, not readily distinguishable from the tips of the umbos Ventral margins of valves strongly crenulated internally Shell with a very fine radial structure Lunule vaguely defined, very slightly sunk, elongate-cordiform, ornamented with a continuation of the concentric lamellae Escutcheon cordiform, slightly sunk, appearing smooth One of the topotypes shows part of the hinge with 5 taxodont teeth posterior and at least 7 anterior to the umbo, the anterior end of the hinge line being broken

Dimensions Holotype length 1 8 mm , height 1 5 mm , thickness (both valves) 1 35 mm

Remarks There does not appear to be any closely related species

Genus *LEIONUCULA* Quenstedt, 1930

(*Geol palaont Abh* **22** (N F , 18), Heft 1, p 112)

Type species *Nucula albensis* d'Orbigny, Albian, original designation

Remarks *Ennucula* Iredale, 1931 and *Leionucula* Quenstedt, 1930 (and possibly also *Nuculopsis* Woodring, 1925 *non* Girty, 1911 *nec* Rollier, 1912) are easily distinguished from *Nucula* by their thin shells and by the absence of any coarse radial shell structure Schenck (1934) placed *Ennucula* as a subgenus of *Nucula*, but it is considered that the genus *Nucula* *sensu lato* is better retained only for those thicker-shelled forms with coarse radial shell structure Thiele (1934, p 786) regarded *Ennucula* as a synonym of *Leionucula*, which seems most probable, they are here regarded as at least congeneric The following three species are referred to *Leionucula* on account of the lack of coarse radial shell structure, the feeble ornament, and the form

LEIONUCULA RAKHIENSIS n sp

(Figures 29*a*, *b*, *c*, plate 10)

Material *Rakhi Nala section Venericardia* Shales (local zone 1) (FB F 1836, the holotype, Reg No L 79825, and many topotypes, 6 of which have been registered, Reg No L 79826–31)

Description No traces of any radial shell structure Shell apparently not very thick, of moderate size, oval-subtriangular in outline, moderately elongate, not very strongly inflated Umbos small, not high, situated posterior to the middle line at about one-third of the length Antero-dorsal margin moderately long, almost straight, very slightly convex, gently descendent Anterior end rather narrowly rounded Ventral margin moderately convex, the convexity appearing to be somewhat variable Posterior end bluntly angular, there being a tendency for the posterior portion of the ventral margin to be more steeply ascendent than the anterior portion Postero-dorsal margin not very short, only moderately steeply descendent, practically straight Surface showing traces of fine concentric threads, which are about half as wide as their intervals, and of very fine growth lines There are 11 threads in 3 mm on the antero-ventral portion of one of the topotypes Lunule long and narrow, moderately depressed as a whole, but projecting along the median line, the projection being more marked away from the umbonal region, outer edge limited by a vague, blunt ridge Escutcheon cordiform, its other characters like those of the lunule Valve margins internally smooth ventrally Traces of taxodont teeth can be seen on the dorsal margins of some of the topotypes Antero-dorsal margin of posterior adductor scar and postero-dorsal margin of anterior adductor scar appearing to have been more impressed than the remainder of their surfaces

Dimensions Holotype length 16 7 mm , height 11 6 mm , thickness (both valves) 6 7 mm

Remarks The specimens are all moulds *Nucula baboensis* J de C Sowerby (1839, p 328, Pl 24, fig 5), from the Khirthar of Baboa Hill, Cutch, is considerably larger, a little more inflated, more triangular, and has higher umbos *N bisulcata* Sowerby as figured by Cossmann & Pissarro (1904*a*, Pl 33, fig 104–2), from the Bartonian of Le Fayel in France, is more convex ventrally, the posterior end being more upturned, in addition to displaying differences in ornament, specimens from the Barton Beds and Bracklesham Beds attain a much larger size (at least 35 mm), are higher, and have a median raised ridge on each half of the lunule

LEIONUCULA PUNJABENSIS n sp

(Figures 7*a*, *b*, *c*, plate 9)

Material *Zindar Pir section* Upper Chocolate Clays (lower part) (local zone 12) (FB F 2535, the holotype, Reg No L 79832)

Description No traces of radial shell structure Shell apparently not very thick, of moderate size, oval-subtriangular, rather high, not very elongate, moderately strongly inflated Umbos distinct, not broad, situated well posterior to the median line at about one-fifth of the length. Antero-dorsal margin only moderately long, gently arched, becoming moderately steeply descendent Anterior end moderately narrowly rounded Ventral margin very strongly convex Posterior end very bluntly angular, the postero-ventral margin being more steeply descendent than the antero-ventral margin Postero-dorsal margin moderately short, slightly concave and very steeply descendent Ornament consisting of fine, distinct, concentric threads which are of the same width as or slightly narrower than their intervals, there are 7 threads in 1 5 mm on the ventral region of the specimen Valve margins ventrally smooth internally Lunule, as it appears on the mould, rather broad for its length, limited externally by a blunt raised ridge, with a blunt raised median ridge on the distal portion of each part Escutcheon narrowly cordiform, rather deeply impressed, limited by a fine, indistinct thread which has a vague, narrow furrow outside it Traces of taxodont teeth can be seen on the dorsal margin

Dimensions Holotype length (restored) 18 3 mm , height 11 5 mm , thickness (both valves) 7 3 mm

Remarks The single specimen is a mould Compared with *Nucula eymari* Cossmann as figured by Oppenheim (1903*a*, p 82, Pl 5, figs 10, 10*a*), from the Upper Mokattam of Egypt, this species is more pointed and less high anteriorly, is slightly larger, the antero-dorsal margin is less angular, the postero-dorsal margin is concave (not convex), and the shell is apparently somewhat more inflated *N michalskii* Sokolow (1905, pp 5, 54, Pl 2, figs 1–4), from the Oligocene of Mandrikowka, is more pointed and projecting posteriorly, and has relatively wider concentric threads and narrower intervals It is more convex ventrally than *N greppini* Deshayes as figured by Canestrelli (1908, p 55, Pl 1, fig 2), from the Oligocene of Laverda

LEIONUCULA PAKISTANICA n sp

(Figures 8*a*, *b*, plate 9)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2571, the holotype, Reg No L 79833, and 2 topotypes, Reg No L 79834–5, FB F 2562, *2*), Upper Chocolate Clays (upper part, local zone 13) (FB F 2519, *2*)

Description Shell moderately large, thin-shelled, subtriangular in outline, not very high, moderately elongate Umbos not high, not very pointed, situated posterior to the median line at about one-third of the length Antero-dorsal margin long, only slightly convex, the convexity most pronounced along the median portion of the lunule, moderately descendent Anterior end narrowly rounded Ventral margin moderately strongly convex, the posterior end not appreciably more steeply descendent than the anterior end Posterior end bluntly rounded, subangular Postero-dorsal margin practically straight, of moderate length, moderately steeply descendent Surface smooth except for microscopic incrementals Valve margins ventrally smooth internally Lunule broadly lanceolate, slightly sunk as a whole, its outer margin limited by a blunt, rounded ridge which merges with the lateral surface of the shell, its median portion distinctly swollen Escutcheon rather narrowly cordiform, ill-defined except near the umbos

Dimensions Holotype length 16 7 mm , height 12 2 mm , thickness (both valves) 7 5 mm

Remarks The ventral margin is considerably less convex than in *Nucula moendis* Oppenheim (1903*a*, p 82, Pl 10, figs 3–3*d*), from the Upper Mokattam of Fajum, Egypt The umbos are higher, the shell is a little more pointed posteriorly, and the junction of the postero-dorsal and postero-ventral margins is not situated so high up compared with *N bisulcata* Sowerby as figured by Cossmann & Pissarro (1904*a*, Pl 33, fig 104–2), from the Bartonian of Le Fayel, France On the other hand, it is less pointed, less elongate, and less cuneiform posteriorly compared with *N bisulcata* Sowerby as figured by Wood (1864, p 109, Pl 18, fig 13) and Dixon (1850, p 170, Pl 2, fig 13), from the Barton Beds of Barton and the Bracklesham Beds of Bracklesham Bay and Whitecliff Bay Specimens of *N bisulcata* from the Barton Beds and Bracklesham Beds attain a much larger size (at least 35 mm), are higher, and have a raised median ridge on each half of the lunule *N baboensis* J de C Sowerby (1839, p 328, Pl 24, fig 5), from the Khirthar of Baboa Hill, Cutch, is considerably larger, higher, and less pointed anteriorly

Family Nuculanidae

Genus *NUCULANA* Link, 1807

(*Beschr nat Samml Rostock*, pt 3, p 155)

Type species *Nuculana rostrata* (Gmelin), Recent, monotypy

Synonym *Leda* Schumacher, 1817 (*Ess nouv Syst* pp 55, 172), type species *Arca rostrata* Chemnitz, Recent = *Mya pernula* Muller, monotypy

Subgenus *SACCELLA* Woodring, 1925

(Miocene Mollusks from Bowden, Jamaica Part 1 Pelecypods and Scaphopods *Publ Carneg Instn*, no 366, p 15)

Type species *Arca fragilis* Chemnitz, Miocene-Recent = *Leda commutata* Philippi = *Lembulus deltoideus* Risso? = *Nuculana acuminata* Eichwald, original designation

Synonym *Ledina* Sacco, 1898 *non* Dall, 1898 (*antea*) (*I Moll terr terz Piem e Lig* **26**, p 53), type species *Leda fragilis* Chemnitz, original designation

NUCULANA (*SACCELLA*) *SILVESTRIS* (Cotter), 1923

References *Leda silvestris* Cotter, 1923 (p 20, Pl 6, figs 4*a*–*c*), Chhibber, 1934 (p 226), Cotter, 1938 (p 69), Mukerjee, 1939 (p 7), Krishnan, 1943 (p 447) ?*Leda virgo* Martin, Pascoe, 1912 (p 139)

Material *Rakhi Nala section Pellatispira* Beds (local zone 15) (FB F 1993, many specimens, of which 10 have been registered, Reg No L 79836–41, FB F 1997, *1*)

Remarks Although the specimens are not particularly well preserved and are somewhat flattened on account of the argillaceous nature of the matrix, they agree well with Cotter's description and illustrations of *Leda silvestris* They are of about the same size and shape, and show distinct indications of the same type of ornament The type locality of Cotter's species is in the Yaw Stage of the Kyutaw Chaung, 2 miles east of Pasok, Burma, this being the only record of the species under its proper name Pascoe's record (1912, p 139) of *L virgo* Martin (a Miocene species) from 1 mile west-south-west of Thayetkwa, near Myaing, Burma, refers to a locality which is probably in the Yaw Stage, not the Pegu System, and the species concerned is probably *Nuculana* (*Saccella*) *silvestris*

NUCULANA (*SACCELLA*)(?) *RAKHIENSIS* n sp

(Figure 9, plate 9)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1842, *1*), Green and Nodular Shales (local zone 4) (FB F 1867, the holotype, Reg No L 79842)

Description Shell of moderate size for the genus, transversely oval Umbonal region somewhat crushed, but umbos probably submedian in position Antero-dorsal and postero-dorsal margins of about the same length, fairly straight, gently descendent Anterior end moderately narrowly rounded Ventral margin moderately convex, internally smooth Posterior end bluntly rostrate, not produced, the tip of the rostrum being situated rather high up Siphonal region vaguely flattened, with no indication left of any radial fold Ornament consisting of distinct but very fine, sharp, narrow concentric threads with wide intervals Although distinct, these threads are so narrow that they show little width, they are spaced ⅜ mm apart on the ventral portion of the holotype

Dimensions The dimensions of the holotype, which do not allow for crushing or the small amount of turning in of the umbo, are length 10 9 mm , height 6 25 mm Measuring from the growth lines, the ratio of length to height is about 2 1 at about half the height of the shell

Remarks The two specimens which were collected are both rather flattened impressions which, however, show sufficient of the outline and ornamentation to warrant description The form and ornament are apparently characteristic Although the hinge teeth are not seen, and although there is no distinct posterior fold, the form suggests a member of the Nuculanidae rather than a tellinid

NUCULANA (*SACCELLA*) *HAMATA* n sp

(Figures 10*a*,*b*,*c*, plate 9)

Material *Rakhi Nala section* Upper Chocolate Clays (upper part, local zone 13) (FB F 1986, the holotype, Reg No L 79843, and 34 topotypes, Reg No L 79844–9), *Zindar Pir section* Upper Chocolate Clays (upper part, local zone 13) (FB F 2520, *1*, FB F 2519, *1*)

Description Very small, of fairly uniform size and shape Umbonal region moderately prominent, rather broad, the umbos having been approximately median in position Antero-dorsal and postero-dorsal margins gently descendent and of approximately the same length, the latter slightly concave, the former more or less straight Ventral margin semicircular Posterior end bluntly pointed, situated high up Anterior end a continuation of the ventral margin, sometimes somewhat truncated, meeting the antero-dorsal margin in a rather obtuse angle, which in the internal moulds has a slight, thin, oblique, rectangular projection The internal moulds also show an umbonally directed, claw-shaped projection from the junction of the postero-dorsal and posterior margins One specimen shows traces of very fine, closely spaced concentric threads All the moulds have elongate depressed areas dorsally, the anterior being a little smaller and more stiffly triangular in outline There appear to have been six posterior hinge teeth and four or five anterior hinge teeth Pallial sinus not observed Valve margins internally smooth

Dimensions Holotype length 1 56 mm , height 1 3 mm , thickness (both valves) 0 85 mm Topotype length 2 0 mm , height 1 5 mm , thickness (both valves) 0 94 mm

Remarks The specimens are all either internal or external moulds The small size and outline are characteristic, as also appears to be the claw-like projection at the posterior end of the dorsal margin of internal moulds *Leda smirna* Dall, from the Eocene of Florida, which is the type species of *Ledina* Dall, is somewhat similar, but in addition to being more elongate, appears to have been smooth *Nuculana* (*Saccella*) *hamata* is placed in the subgenus *Saccella* on account of the presence of concentric ornament, it being considered that the rostral fold is not preserved on the moulds

NUCULANA (*SACCELLA*) *PAKISTANICA* n sp

(Figures 11*a*, *b*, plate 9)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1967, the holotype, Reg No L 79850), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2571, *2*, FB F 2564, *1*, FB F 2562, *2*)

Description Transversely oval, not very strongly inflated Umbos small, low, not at all prominent Antero-dorsal and postero-dorsal margins practically straight, of almost the same length, at only a small angle to the horizontal Anterior end moderately narrowly rounded Ventral margin gently to moderately convex Posterior end moderately bluntly pointed, rostrate, the rostrum being situated rather high up Surface ornamented with prominent, very closely spaced, fine, concentric threads, which are of about the same width as their intervals, there are about 15 threads in ¾ mm on the ventral portion of the holotype, and they become gradually more closely spaced towards the umbos Lunule indistinct Escutcheon long and narrow, limited by a fine furrow Siphonal region of shell broadly and gently excavated in contradistinction to the moderately convex median portion of the shell Valve margins internally smooth Traces of taxodont dentition are seen showing through the dorsal margins of the shell

Dimensions Holotype length (restored) 3 75 mm , height 2 0 mm , thickness (both valves, estimated) 0 5 mm Ratio of length to height at about half the height of the shell, based on growth lines, 1 85 1

Remarks This species is not so high, has less conspicuous umbos, a less conspicuous lunule, is more elongate, and apparently has more crowded and more distinct concentric ornament, compared with *Nuculana* (*Saccella*) *silvestris* (Cotter) *Leda accepta* Liverowskaja (1939, p 155, Pl 1, figs 4, 5), from the Oligocene of Yergheny (Russia), is similar but about three times as large The Rakhi Nala form is less convex ventrally than fig 7 of Speyer's illustration of *L gracilis* Deshayes, from the Chattian of Cassel (1884, Pl 17, figs 6–11), and the umbonal angle is wider, the posterior keel less distinct, and the postero-ventral margin not sinuous as compared with the same species as figured by Wolff, from the Oligocene of southern Bavaria (1897, p 235, Pl 21, fig 5) *L haunsbergensis* Traub (1938, p 44, Pl 2, figs 3*a*, *b*), from the Palaeocene of Austria, has a more convex ventral margin

NUCULANA (*SACCELLA*) *SEMIBISTRIATA* n sp

(Figure 12, plate 9)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 4) (FB F 1842, 2, Reg No L 79852–3, FB F 1867, the holotype, Reg No L 79851), *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, 2)

Description Shell oval, moderately distinctly rostrate posteriorly, gently inflated Umbos not prominent, submedian, situated slightly anterior to the median line at about seven-seventeenths of the length Antero-dorsal margin slightly convex, not very long, gently descendent Anterior end rounded Ventral margin moderately strongly convex, a little attenuated posteriorly Posterior end rostrate, the rostrum short and rather bluntly pointed Postero-dorsal margin moderately long, slightly concave, gently descendent Lunule and escutcheon not seen There is a vague indication of a slight, wide, radial furrow from the umbonal region to the antero-ventral corner Ornament consisting of a very distinctive arrangement of concentric, incised lines These are closely spaced on the posterior and ventral portions of the shell, but alternate ones die out anteriorly and dorsally from a line running approximately from the middle of the postero-dorsal margin to the antero-ventral corner The actual line of demarcation is not at all sharp The incised concentric lines are thus about twice as widely spaced on the antero-ventral portion of the shell as on the postero-ventral portion, they are also about twice as widely spaced on the umbonal region as on the antero-ventral margin There are 13 or 14 incised lines in ¾ mm near the ventral margin, 5 in ¾ mm in the umbonal region, and about 9 in ¾ mm at the anterior end

Dimensions Holotype length 6 4 mm , height 4 0 mm

Remarks *Leda haunsbergensis* Traub (1938, p 44, Pl 2, figs 3*a*, *b*), from the Palaeocene of Austria, has a less convex ventral margin, and is, moreover, ornamented with solid concentric threads which on the ventral region are flat, with intervals four or five times as wide, the siphonal area of the Austrian species is smooth *L effossa* von Koenen (1892, p 260, Pl 15, figs 3–5), from the Lower Tertiary (Bohrloche Schichte) of Lichterfelde near Berlin, is a little less convex ventrally and is also smooth except for some growth lines Compared with fig 7*b* of Speyer's illustration of *L gracilis* Deshayes, from the Chattian of Cassel (1884, Pl 17, figs 6–11), the Rakhi Nala fossil does not have raised concentric threads, its ornament is weaker, and it has no distinct keel, and is somewhat less transverse

NUCULANA (*SACCELLA*) *PUNJABENSIS* n sp

(Figures 13*a*, *b*, plate 9)

Material *Zindar Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2539, the holotype, Reg No L 79854)

Description Shell small, strongly inflated, outline oval-subquadrate, although the rostral region is slightly broken Umbos not very prominent, distinct, submedian Antero-dorsal margin rather short, very slightly convex, gently descendent Anterior end rather broadly rounded Ventral margin convex, distinctly upturned laterally Posterior end appearing obliquely truncated on account of being slightly broken, but the ornament shows that it was bluntly rostrate, the tip of the rostrum being situated rather high up Postero-dorsal margin gently concave, a little longer than the antero-dorsal margin and a little more descendent Ornament consisting of very fine, closely spaced concentric threads of which there are about 15 in ½ mm on the ventral portion of the shell, these threads are a little more closely spaced near the ventral margin Characters of lunule and escutcheon not determinable

Dimensions Holotype length 2 6 mm , height 1 9 mm , thickness (both valves) 1 5 mm

Remarks *Leda pyramidata* Cuvillier (1935, p 10, Pl 1, figs 23, 24), from the Bartonian of Egypt, is more cuneiform, less inflated, and relatively longer and less high posteriorly *L brevis* von Koenen (1893, p 1122, Pl 75, fig 4), from the Lower Oligocene of Wolmirsleben, is more elongate, has a more produced rostrum and more conspicuous umbos *L nana* von Koenen (1893, p 1128, Pl 75, figs 12–15), from the Lower Oligocene of Lattorf, is smaller, less rectangular in outline, with a more convex ventral margin and less conspicuous ornament *L costulata* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 33, fig 105–2), from the Bartonian of Acy (France), is larger, more elongate, and more heavily sculptured The strong inflation, subrectangular form and fine ornament of the Zinda Pir form are apparently characteristic

NUCULANA (*SACCELLA*) *UMBONI-INFLATA* n sp

(Figures 14*a*, *b*, plate 9)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2539, the holotype, Reg No L 79855, and 1 topotype, Reg No L 79856, FB F 2536, *2*), Upper Chocolate Clays (upper part, local zone 13) (FB F 2519, *2*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2508, *1*)

Description Shell of moderate size for the genus, transversely subelliptical, elongate, rostrate, strongly inflated, especially in the umbonal region Umbos only moderately prominent, rather broad, median in position Antero-dorsal margin long, slightly convex, only slightly descendent Anterior end rather narrowly rounded Ventral margin gently convex, slightly emarginate towards the posterior end adjacent to the rostrum Posterior end rostrate, produced, the tip appearing narrow and vertically truncated Postero-dorsal margin long, slightly concave, only slightly more steeply descendent than the antero-dorsal margin Ornament consisting of closely spaced, distinct concentric threads which are of the same width as or slightly wider than their intervals, there are 12 in ½ mm on the central portion of the shell Valve margins internally smooth Characters of lunule and escutcheon not determinable, since the hinge teeth show through where the shell has been somewhat worn dorsally

Dimensions Holotype length 6 0 mm , height 3 5 mm , thickness (both valves) 3 0 mm

Remarks Although this form has the same type of ornament and is strongly inflated like *Nuculana* (*Saccella*) *punjabensis*, it is more narrowly rounded anteriorly and very much more produced and rostrate posteriorly Compared with *Leda striata* Lamarck as figured by Frauscher (1886, p 139, Pl 6, fig 23), from the Parisian of the northern Alps, and by Cossmann & Pissarro (1904*a*, Pl 33, fig 105–1), from the Lutetian of Parnes and from the

Cuisian, the Zinda Pir form is more elongate, more corbuliform, more rostrate, has a distinct emargination of the ventral region just anterior to the rostrum, and has broader and less elevated umbos *L galeottiana* Nyst as figured by Cossmann & Pissarro (1904*a*, Pl. 33, fig 105–4), from the Lutetian of Damery and from the Bartonian, is somewhat similar, but has a distinctly more transverse appearance, since the convexity of the ventral margin has no posterior emargination, and the shell has a more pointed rostrum, the French form also has smaller and more distinct umbos, and is not so large

NUCULANA (*SACCELLA*) *SORIENSIS* n sp

(Figures 15*a*,*b*, 16*a*,*b*, plate 9)

MATERIAL *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 79857, and 8 topotypes, Reg No L 79858–63, FB F 2676, 2 small specimens, Reg No L 79864–5)

DESCRIPTION Shell suboval, not elongate, with a short rostrum posteriorly, moderately inflated Umbos small, pointed, not prominent, submedian Antero-dorsal margin only moderately long, almost straight, only gently descendent Anterior end rounded Ventral margin strongly convex, only young specimens showing a slight emargination posteriorly Posterior end with a short, pointed rostrum which is situated high up Postero-dorsal margin straight, moderately long, only gently descendent Ornament consisting of fine, sharp concentric threads which are about half the width of their intervals on the holotype and on the majority of the topotypes, there are about 10 in $\frac{1}{2}$ mm on the ventral portion of the holotype On some of the topotypes the threads appear relatively broader, but this is probably due to wear Lunule indistinct Escutcheon long and narrow, limited externally by a fine, sharp carina which runs from the umbo to the tip of the rostrum, this carina keeps close to the postero-dorsal margin, and the concentric ornament apparently does not pass over it Normal type of taxodont teeth can be seen on the holotype and four of the topotypes Siphonal region very vaguely depressed

DIMENSIONS Holotype height 2 5 mm , length (restored) 5 0 mm Ratio of length to height measured on concentric threads of holotype, 1 9 1

REMARKS This species is more convex ventrally, and has a more distinct posterior keel, and sharper and wider spaced ornament than *Nuculana* (*Saccella*) *pakistanica* It is closely related to *N* (*Saccella*) *striata* (Lamarck)—recorded as *Nucula striata* by Nyst (1843, Pl 17, fig 4), from the Tertiary of Belgium, as *Leda striata* by Deshayes (1829, p 236, Pl 42, figs 4–6), from the Eocene of the Paris Basin, and by Cossmann & Pissarro (1904*a*, Pl 33, fig 105–1), from the Lutetian of Parnes and from the Cuisian, and as *Nuculana striata* by Cossmann & Pissarro (1903, p 32, Pl 4, figs 17, 18), from the Eocene of Fresville (Cotentin), and by Cossmann (1904, p 206, Pl 7, figs 25–28), from the Eocene of Bois-Gouet and Arthon The present species, however, has a straighter dorsal margin, the umbos being less conspicuous, the concentric threads seem to have distinctly wider intervals, the posterior carination is quite sharp, and the tip of the rostrum is more sharply pointed. The rostrum is shorter and the oblique posterior furrow is more vague than in *Leda crispata* von Koenen var. *ukrainica* Sokolow (1905, pp 7, 55, Pl 1, figs 4–9), from the Oligocene of Mandrikowka

The umbos are less prominent and the ventral margin more convex than in *Nucula westendorpii* Nyst (1843, Pl 15, fig 9), from the Tertiary of Belgium *Leda gracilis* Deshayes (1860, p 831, Pl 64, figs 24–26), from the Fontainebleau Sands of Jeures, Etréchy and Morigny and from the Tertiary of Neucul, Délémont (Switzerland) and Kunfungen near Cassel—also recorded by Wolff (1897, p 235, Pl 21, fig 5), from the Oligocene of Thalberggraben near Siegsdorf (southern Bavaria)—is a little more elongate, and the postero-ventral margin is somewhat emarginate *L crispata* von Koenen (1893, p 1119, Pl 75, figs 5–7), from the Lower Oligocene of Lattorf, has an emarginate postero-ventral margin, and the rostrum is differentiated by a radial depression *L perovalis* von Koenen (1893, p 1123, Pl 75, figs 2, 3), from the Lower Oligocene of Wolmirsleben and Unseburg, has a less pointed rostrum and more projecting umbos The Zinda Pir species is less inflated, less elongate, has less prominent umbos, and possesses more widely spaced concentric threads than *Nuculana* (*Saccella*) *silvestris* (Cotter)

Family SOLEMYIDAE

Genus *SOLEMYA* Lamarck, 1818

(*An s Vert* **5**, 488)

TYPE SPECIES '*Solenomya mediterranea*' Lamarck, Recent = *Solemya mediterranea* Lamarck = *Tellina torgata* Poli, Children, 1823

SYNONYMS *Solenimya* Bowdich, 1822 (*Elem Conch* **2**, 8) (error)

Solenomya Children, 1823 (*Quart J Sci* (*R Inst*), **14**, 300) (*em pro Solemya*)

Stephanopus Scacchi, 1833 (*Oss Zool* **1**, 5), type species *Stephanopus polianus* Scacchi, Recent, monotypy

SOLEMYA INSIGNIFICA n sp

(Figure 30, plate 10)

MATERIAL *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1845, *1*, FB F 1860, the holotype, Reg No L 79866)

DESCRIPTION Shell transversely oval-oblong in outline, preserved as a flattened impression, but evidently very little inflated in its natural state Umbos not prominent, small, situated posterior to the median line at about seven-ninths of the length Ends rounded, the anterior end a little more sharply so Antero-dorsal margin long and fairly straight, only slightly descendent Postero-dorsal margin more convex, rather rapidly merging with the posterior end Ventral margin almost straight and horizontal Along the ventral margin, particularly near the posterior end, there are indications of numerous very fine radial riblets which are evidently not due to the state of preservation

DIMENSIONS Holotype length 18 2 mm , height 8 0 mm

REMARKS *Solenomya angusta* (Deshayes) as figured by Cossmann (1905, p 141, Pl 9, figs 24, 25), from the Eocene of Bois-Gouet, is smaller, has a more sharply rounded anterior end, and is apparently a little more inflated *Solemya cuvieri* Deshayes (1860, p 731, Pl 7, figs 16, 17), from the Calcaire Grossier of Damery, Parnes, Mouchy, Ver and Ermenonville, which also has fine radial ornament, has a more elongate anterior end

Order ARCACEA

Superfamily Arcacea

Family Arcidae

Genus *BARBATIA* Gray, 1847

(*Proc Zool Soc Lond* **15**, 197)

Type species *Arca barbata* Linné, Middle Miocene-Recent, monotypy and original designation

Synonym *Barbatia* Gray, 1842 (*Syn Cont Brit Mus* 44th ed p 81) (*nomen nudum*)

Subgenus *PLAGIARCA* Conrad, in Kerr, 1875

(*Geology of N Carolina*, **1**, app A, p 4, Pl 1, fig 11)

Type species *Barbatia carolinensis* Conrad, Upper Cretaceous, monotypy

BARBATIA (*PLAGIARCA*) *PSEUDONAVICULA* n sp

(Figures 17*a*, *b*, plate 9)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1967, the holotype, Reg No L 79867, and 7 topotypes, Reg No L 79868–70) (N B The holotype consists of two spread-eagled valves)

Description Shell small, arciform, transversely subquadrate, elongate, with a wide but distinct median byssal depression, rather strongly inflated Umbos rather broad, not very prominent, situated anterior to the median line at about one-quarter of the length of the shell Hinge line quite straight, equal to or only very slightly less than the total length of the shell Anterior end gently convex, gradually falling away from the point where it meets the hinge line Ventral margin long, subparallel to the hinge line, slightly emarginate in its median portion corresponding with the byssal depression Posterior end nearly straight and vertical, sometimes very slightly emarginate and alate Both anterior and posterior ends meet the hinge line at an angle of about 90° It has only been possible to develop the hinge on one of the topotypes, it does not show the characters well, but the cardinal area is extremely narrow, and the hinge teeth are of the usual taxodont type, close together and vertical, becoming somewhat oblique (upper ends farther from umbo) towards the ends of the hinge line, which is long and straight Ornament consisting of about 54 radial ribs, on the posterior flattened wing the ribs are less distinct, flatter, and considerably wider than their intervals, on the remainder of the surface they alternate in size fairly regularly, are finely but distinctly beaded, and on the average only a little wider than their intervals, if at all Posterior part of shell slightly higher than the anterior

Dimensions Holotype length 6 0 mm , height 2 5 mm

Remarks The almost complete absence of a cardinal area removes this form from *Barbatia*, *sensu stricto* Although the form is more transverse, the ventral margin less convex, and there is a broad, shallow, distinct byssal depression compared with *B* (*Plagiarca*) *carolinensis* Conrad, the Rakhi Nala fossil shows some resemblance to forms from the Eocene of the Paris Basin which were placed in the subgenus *Plagiarca* by Cossmann & Pissarro (1904*a*) *Arca* (*Plagiarca*) *angusta* Lamarck as figured by Cossmann & Pissarro (1904*a*, Pl 36, fig 110–40), from the Lutetian of Villiers, is still more transverse, has finer ornament, and does not show such a byssal depression *A* (*Plagiarca*) *lucida* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 36, fig 110–41), from the Lutetian of Parnes, is also somewhat more transverse, the ornament is indistinct, and the byssal depression is scarcely seen

Family GLYCYMERIDAE

Genus *GLYCYMERIS* Da Costa, 1778

(*Brit Conch* p 168)

TYPE SPECIES *Glycymeris orbicularis* Da Costa, Recent = *Arca glycymeris* Linné, by tautonymy, and Bucquoy, Dollfus & Dautzenberg, 1891

SYNONYMS *Tuceta* Bolten, in Roding, 1798 (*Mus Bolt* pt 2, pp 172, 173), type species *Tuceta pilosa* Bolten, Recent = *Arca pilosa* Linné, Dall, 1909

Pectunculus Lamarck, 1799 (*Mem Soc Hist nat Paris*, p 87), type species *Arca pectunculus* Linné, Recent, monotypy

Pectunculigenus Renier, 1807 (*Tav serv Classif Conn Anim* Tabell vii) (= *Pectunculus* Lamarck)

REMARKS '*Pectunculi*' Huddersford, 1770 is a vernacular name, and *Axinaea* Poli, 1791 and *Axinaeoderma* Poli, 1795 are not binomial From time to time the above names have been misspelt *Axinaeoderm* (Poli, 1795), *Axinea* (Rafinesque, 1815), *Axinea* (Griffith, 1834), *Petunculus* (Quoy & Gaimard, 1835), *Axinoderma* (Herrmannsen, 1846), *Pectunculis* (Conrad, 1860), *Pectundulus* (Tate, 1882), *Axinia* (Dautzenberg, 1893), *Glycimeris* (Zittel) and *Glicymeris* (Maury, 1924)

GLYCYMERIS(?) *SORIENSIS* n sp

(Figures 18*a*, *b*, plate 9)

MATERIAL *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2539, the holotype, Reg No L 79874)

DESCRIPTION Shell moderately small, a little broken anteriorly and posteriorly, valves slightly crushed together and slid across each other Rather strongly inflated, especially umbonally Growth lines show that the shell was suborbicular in outline, with relatively prominent umbos submedian in position Both radial and concentric ornament are present Radial ribs fine, sharp, considerably narrower than their intervals, fainter anteriorly and posteriorly, and almost entirely obsolete ventrally, usually arranged in three orders, although in one place there are two secondary threads between adjacent primaries, there are about 8 primary threads Concentric ornament of fine threads of about the same width as their intervals, sharp and distinct between the ribs on the anterior part of the shell, but fainter, blunter, and more rounded elsewhere, there are about 11 to the mm ventrally Radial ornament more prominent than the concentric in the earlier part of the shell, concentric ornament more prominent than the radial in adult portion of the shell Concentric ornament itself less conspicuous in the early part of the shell than later

Dimensions Holotype length 4 9 mm , height 4 9 mm , thickness (both valves) 3 0 mm

Remarks This species is provisionally placed in the genus *Glycymeris* on account of some resemblance to *G jacquoti* (Tournouer) While exhibiting some resemblance to some forms placed in the subgenus *Pectunculina* d'Orbigny, 1844 of the genus *Limopsis* Sasso, 1827 of the family Limopsidae, its ornament is of a different type from that encountered in *Glycymeris*, *Grandiaxinaea* Iredale, 1931, *Melaxinaea* Iredale, 1931, *Glycymerella* Woodring, 1925, *Axinactis* Morch, 1861, *Glycymerita* Finlay & Marwick, 1937, *Glycymerula* Finlay & Marwick, 1937, *Manaia* Finlay & Marwick, 1937, *Pseudaxinea* Monterosato, 1892, *Tucetilla* Iredale, 1939, *Tucetona* Iredale, 1931, *Tucetopsis* Iredale, 1939 or *Veletuceta* Iredale, 1931

Pectunculus jacquoti Tournouer as figured by Oppenheim (1901*a*, p 152, Pl 4, figs 8, 9), from the Priabonian of Via degli Orti, and by Cossmann (1922*a*, p 132, Pl 8, figs 31–34), from the Bartonian of Côte des Basques (Biarritz) and the Auversian of Lady Bruce (Biarritz), is larger, has more widely spaced primary ribbing, and the ribbing reaches the ventral margin The illustration given by Dreger (1903, p 265, figs *a*, *b*, *c*) of ?*P nobilis* Guembel, from the Eocene of Haring in the Tyrol, is of a more transverse form, the concentric ornament not consisting of such definite closely spaced raised threads ventrally, and the radial ornament being uniform and more widely spaced

GLYCYMERIS sp A

(Figure 31*a*, *b*, *c*, plate 10)

Material *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 79875)

Description Very small, suborbicular, moderately inflated Umbos small, not prominent, submedian There seem to be traces of a small cardinal area About 12 sharp, fine, distinct radial ribs about half as wide as their intervals No concentric ornament seen

Dimensions Holotype length 0 75 mm , height 0 75 mm , thickness (both valves) 0 5 mm

Remarks This is probably an immature specimen The probable presence of a small cardinal area combined with the rather erect umbos precludes placing it in the genus *Venericardia* It is very much smaller and has thicker ribs and narrower intervals compared with *Pectunculus deletus* (Solander, in Brander) as figured by Wood (1864, p 97, Pl 16, fig 3), from the Eocene of Barton

Family Noetiidae

Subfamily Noetiinae

Genus *NOETIA* (Gray, 1842) Gray, 1857

(*Ann Mag Nat Hist* ser 2, 19, 371)

Type species *Noetia triangularis* Gray, Recent=*Arca reversa* (Gray MS) Sowerby, monotypy.

NOETIA MAGNIFICA n sp

(Figures 19*a*, *b*, 20, plate 9)

Material Lower Chocolate Clays the holotype (Reg No L 77886) and 1 topotype (Reg No L 77887) from east of Safaed, south of Tobah, Dera Ghazi Khan District, Punjab *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1938, 4 moulds, Reg No L 79887–80), Lower Chocolate Clays (local zone 10) (FB F 1966, 2, Reg No L 79876), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2556, 2)

Description Shell transversely oval-subtrapezoidal, strongly inflated, rather produced postero-ventrally Umbos distinct, prominent, opisthogyrous, submedian in position, only very slightly anterior to the median line, only moderately high on account of the form of the shell, subcarinate on their posterior side Hinge line almost straight, considerably shorter than the greatest length of the shell Antero-dorsal margin short, straight, slightly descendent Anterior end rounded, sweeping well in towards the umbos to join the antero-dorsal margin Ventral margin gently convex, straighter in its posterior part Posterior end obliquely truncated, gently convex, meeting the ventral margin in a rather sharp curve and the postero-dorsal margin in a regular curve Postero-dorsal margin short, almost straight, slightly angulated medially, gently descendent Surface ornamented with 39 radial ribs which are of the same width as or slightly narrower than their intervals, the posterior rib is bifurcate All ribs finely but distinctly beaded by accentuated, rather scaly growth lines in the early stages, as the shell grows, the beading becomes obsolete and the ribs relatively less elevated Surface with a rounded carination running from the umbo to the postero-ventral corner, the carination becoming less sharp with age Valve margins internally coarsely fluted Cardinal area consisting of two parts Anterior part narrowly dagger-shaped, sharply pointed anteriorly, bluntly pointed posteriorly, the posterior end being situated a little posterior to the umbos at an angle of about 45° from the tips of the umbos it carries 47 vertical ligament grooves usually somewhat narrower than their intervals and which occasionally bifurcate and often appear double when worn, it is flat posteriorly and sunk anteriorly Posterior part of cardinal area consisting of a broad cordiform lunule-like escutcheon A narrow band parallel to the posterior end of the striated ligament area is rather raised and is bordered by a fine incised line, and the posterior half of the remaining surface bears two bifurcate radial ribs near the commissure of the valves, the most posterior one forming a very obtuse angulation of the outline

Moulds from some of the softer consolidated calcareous muds are often considerably distorted and appear much more elongate, the cardinal area also loses its characteristic appearance and looks rather like that of an *Arca*

Dimensions Holotype length 29 1 mm , height 24 1 mm , thickness (both valves) 20 9 mm An internal mould from FB F 1938 has the following dimensions length 27 1 mm , height 18 0 mm , thickness (both valves) 14 8 mm

Remarks The holotype has been selected from some specimens collected by Mr Pinfold since they are better preserved

Arca (*Anadara*) *molengraaffi* Martin, from the Upper Eocene of Nanggulan, Java (1915, p 184, Pl 7, figs 191, 191*a*, 191*b*, 192, 192*a*), redescribed and figured by MacNeil (1938, p 30, Pl 4, figs 22, 23), while possessing about the same number of ribs has a more elevated umbonal region and is consequently less transverse, its ribs do not appear to be beaded, and the posterior area is a little more distinct

Subfamily STRIARCINAE

Genus *ARCOPSIS* von Koenen, 1885

(*Abh Ges Wiss Göttingen*, Phys Kl, **32**, Th 2, p 86)

TYPE SPECIES *Arca limopsis* von Koenen, Palaeocene, Reinhart, 1935

SYNONYM *Fossularca* Cossmann, 1887 (*Ann Soc Roy Malac Belg* ser 4, **2**, 138), type species *Arca quadrilatera* Lamarck, Eocene, original designation

ARCOPSIS SPARSIINCISA n sp

(Figures 21 *a*, *b*, plate 9)

MATERIAL *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 13) (FB F 2519, the holotype, Reg No L 79881)

DESCRIPTION Shell transversely oval-subrectangular, moderately strongly inflated, with a vague, wide, median, byssal depression Hinge line straight, not forming quite the whole width of the shell Umbos moderately prominent, rather broad, situated at approximately one-third of the length, and anterior to the median line Anterior end rounded According to the trend of the concentric ornament, the ventral margin was practically straight, almost parallel to the hinge line, very slightly descendent in a posterior direction Posterior end slightly arched, sloping upwards slightly towards the umbos, meeting the umbos at an angle of a little more than 90°, and joining the ventral margin in a rounded curve Ornament consisting of radial riblets and concentric incised lines Nearly 60 fine radial riblets, slightly narrower than or equal to the width of their intervals, and rather sharp on the extreme anterior and posterior portions of the surface, but rather flat and a little wider than their intervals on the rest of the surface, they are not beaded Concentric ornament consisting of fine concentric threads on the extreme anterior portion of the surface, giving place to fine incised lines on the remainder of the surface Threads on the anterior portion forming a delicate, wide-meshed, reticulate network with the riblets, there appear to be minute crenulations at the points of intersection Threads gradually becoming more widely spaced as they change into incised lines, the latter are quite widely spaced (8 in $\frac{1}{2}$ mm on the postero-ventral portion of the specimen), and are occasionally not parallel Hinge line broken, but there are 7 small taxodont teeth remaining posterior to the umbo Cardinal area only preserved posterior to the umbo, where it is seen to be a narrow, deeply excavated surface with one stria, that part of the excavation which borders the lateral surface of the shell being steep and slightly undercut A broadly triangular portion is broken away from beneath the umbo

DIMENSIONS Holotype length of fragment 2 4 mm, height of fragment 1 9 mm, thickness of fragment (one valve) 0 9 mm

REMARKS The single specimen is broken, not even the ventral margin being intact, but the form and ornament can be discerned so well that the species is described It is placed in the genus *Arcopsis* on account of the subquadrate outline, fine ornament and narrow cardinal area *Arca esnaensis* Newton (1898, p 538, Pl 19, figs 15, 16), from the Libyan of Egypt, is distinctly larger, has distinctly beaded ribs, and a less distinct median byssal depression *A decussata* Nyst (1843, Pl 16, fig 11), from the Tertiary of Belgium, also recorded by Speyer (1884, Pl 21, fig 2) from the Middle Oligocene of Ob -Kaufungen, lacks the radial byssal depression, has narrower and more prominent umbos and more closely spaced concentric ornament. *A distinctissima* Mayer-Eymar as figured by Frauscher (1886, p 125, Pl 6, fig 17), from the Parisian of the northern Alps, is much larger, more elongate, and has rather different ornament

ARCOPSIS(?) sp A

(Figures 22*a*,*b*, plate 9)

MATERIAL *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 79882, and 1 topotype, Reg No L 79883)

DESCRIPTION Shell small, subquadrate, posterior end of holotype broken, but shell apparently about as high as wide Moderately inflated, more or less equilateral Umbo small, moderately prominent, gently prosogyrous, apparently submedian Hinge line straight, appearing about as long as the shell on the holotype, but slightly shorter on the smaller, crushed topotype Anterior end vertical, almost straight, very slightly convex Ventral margin horizontal, almost straight, very slightly convex, meeting the anterior margin in a rounded angle of about 90° The topotype appears broadly oval except for the straight hinge line Cardinal area long, narrowly triangular, at right angles to the plane of commissure of the valves The hinge shows 7 small taxodont teeth anterior to the umbo, these teeth appear to become a little divergent at the extremity of the hinge line At first sight the surface appears to be smooth, but there are microscopic closely spaced concentric threads and traces of very vague, fine radial ornament on the more mature part of the shell

DIMENSIONS Holotype length (incomplete) 1 3 mm , height 1 5 mm , thickness (one valve) 0 37 mm Topotype length 1 05 mm , height 0 9 mm

REMARKS This form is provisionally placed in the genus *Arcopsis* on account of the form, weak ornament, and nature of the cardinal area and hinge line The two specimens available are evidently immature

Family CUCULLAEIDAE

Genus *CUCULLAEA* Lamarck, 1801

(*Syst anim* p 116)

TYPE SPECIES *Cucullaea auriculifera* Lamarck, Recent = *Arca cucullata* Chemnitz = *A cucullus* Gmelin = *Cucullaea concamerata* (Martini), Schmidt, 1818, and Children, 1823

CUCULLAEA(?) sp A

(Figures 32*a*,*b*, plate 10)

MATERIAL *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 79884)

DESCRIPTION Shell very small, moderately inflated, equivalve, obliquely suboval with a straight hinge line Umbos small and low, not at all swollen, incurved, and situated slightly anterior to the middle line Hinge line straight, a little shorter than the greatest length of the shell Anterior end gently convex, extending only slightly farther forward than the anterior end of the hinge line, and receding into the ventral margin in a regular, shallow curve Ventral margin strongly convex, a little less so in its anterior portion where it merges into the anterior end Posterior end straight to slightly convex, meeting the posterior end of the hinge line at an angle of about 120°, and meeting the ventral margin in a sharp but well-rounded curve, postero-ventral portion of the shell gently drawn out Ornament consisting of between 30 and 40 (nearer 40) fine radial threads, very little elevated, and of about the same width as their intervals There is no concentric ornament, but occasional growth lines can be determined Cardinal area not well preserved, apparently not wide, and as long as the hinge line

DIMENSIONS Holotype length 1 05 mm , height 0 9 mm , thickness (both valves) 0 7 mm

REMARKS This form has been provisionally regarded as an immature *Cucullaea* in spite of its superficial resemblance to some forms of *Bathyarca* and *Boussacia* *Bathyarca* is inequivalve, with the left valve larger than the right valve, and has a distinct concentric ornament *Boussacia* is also inequivalve, and is more modioliform, the area being reduced to an oblique furrow The internal characters of the Zinda Pir specimen are not seen so that the hinge cannot be compared with that of *Bathyarca* and *Boussacia*, neither is it known whether the valve margins were internally smooth as in *Boussacia* or internally crenulated as in *Bathyarca* The inflation is rather low for a *Bathyarca*

Arca (?*Anadara*) *heterosculpta* Traub (1938, p 47, Pl 2, figs 10*a*–*d*), from the Palaeocene of Austria, although possessing a somewhat similar right valve, has quite a different left valve, even the right valve is less obliquely oval (the ventral and posterior margins joining in a more angular curve) and is higher anteriorly, and has more distinct concentric ornament *A saxonica* von Koenen (1893, p 1107, Pl 73, figs 9–12), from the Lower Oligocene of Calbe, Atzendorf and Unseburg, is less obliquely drawn out in a postero-ventral direction, the ventral margin being more regularly semicircular, and the shell more inflated *Pectunculus* (*Boussacia*) *aviculoides* (d'Archiac) as figured by Cossmann (1922*a*, p 135, Pl 8, figs 43–46), from the Bartonian of Biron (near Orthez) and the Côte des Basques (Biarritz), is also somewhat similar, but is higher and has fine reticulate ornament

Order DYSODONTA

Superfamily PTERIACEA

Family VULSELLIDAE

Genus *VULSELLA* Bolten, in Roding, 1798

(*Mus Bolt* pt 2, p 156)

TYPE SPECIES *Vulsella major* Bolten, Recent = *V vulsella* (Linné), Prashad, 1932.

SYNONYMS The following are usually regarded as synonyms

Vulsella Lamarck, 1799 (*Syst anim* p 133), type species *V lingulata* Lamarck, Recent = *Mya vulsella* Linné, monotypy

Reniella Swainson, 1840 (*Treat Malacol* p 386), type species *R dilatata* Swainson, Recent, monotypy

Baphia (Gevers, 1787) Gray, 1847 (*Proc Zool Soc Lond* 15, 199), type species. *Mya vulsella* Linné, Recent, monotypy

Abisa de Gregorio, 1884 (*Bull Soc malac Ital* 10, 57), the type species, if not already designated, should be selected from the following ten recent species in the original list *Vulsella navicula* de Gregorio, *V claripta* de Gregorio, *V valida* de Gregorio, *V tigrina* de Gregorio, *V pulchella* de Gregorio, *V ringella* de Gregorio, *V cimbula* de Gregorio, *V scrobula* de Gregorio, *V umbotropa* de Gregorio and *V cochlearina* de Gregorio

Vulsellopsis Douvillé, 1907 (*Ann Paléont* 2, 113), type species *Vulsella caillaudi* Zittel, Lower Eocene, original designation

VULSELLA PAKISTANICA n sp

(Figures 33*a*, *b*, plate 10)

Material *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1932, the holotype, Reg No L 79885, and 1 fragmentary topotype, Reg No L 79886)

Description Shell of moderate size, ostreiform, linguiform, high, little inflated, ventral portion of shell curved sideways to the right at an angle of about 30°, valves not in contact along the posterior side Umbos moderately prominent and pointed, that of the right valve the higher, situated a little posterior to the middle line Ventrally the shell is a little twisted posteriorly Umbos not very close to each other, sufficiently far apart to display the triangular ostreiform ligament area Although the shell is elongate-oval in outline in a vertical direction, the apex is rather pointed and there is a convex projection on the anterior margin just below the middle Ornament consisting of distinct, strong, scaly lamellae with gently concave intervals, these lamellae, especially in the earlier stages of growth, are frilled, the frills being due to indentations in the outline of the lamellae and not to radial ornament Lamellae spaced about 2 mm apart in the middle part of the shell but tending to be more closely spaced ventrally and even closer anteriorly and posteriorly Right valve appearing to be slightly larger than the left

Dimensions Holotype length 27 4 mm , height 58 8 mm , thickness (both valves, measured along the plane of commissure) 20 6 mm

Remarks The species is not quite so regularly narrow, the postero-dorsal and postero-ventral margins are not alate, and the concentric lamellae are distinctly frilled compared with *Vulsella legumen* d'Archiac & Haime (1854, p 276, Pl 24, fig 13), from the Upper Ranikot of Sind, Laki of Sind (holotype), and Khirthar of the Mari Hills, western Sind, Cutch and Surat No other Eogene species seems to be closely comparable

VULSELLA GRANDICUBITUS n sp

(Figures 34*a*, *b*, plate 10)

Material *Zinda Pir section* White Marl Band (local zone 11) (FB F 2734, the holotype, Reg No L 79887, and 12 topotypes, Reg No L 79888–93)

Description Shell of large size, smooth except for growth lines, internally subnacreous, subequivalve, flattened, slightly more inflated in the younger stages The mode of preservation does not allow of determining if any gape was present Outline peculiar, for about the first half of its life the outline of the shell remained elongate-oval in a vertical direction, but later the direction of growth changed so that the axis is directed antero-ventrally at an angle of about 45° to the horizontal That the direction is antero-ventral is confirmed by the fact that, in the earlier stages, one side is gently convex (the anterior), and the other is more or less straight and vertical (the posterior), the same condition as is found in many Recent species Umbos opisthogyrous Ventral outline sharply and narrowly rounded, its culmination, as indicated by the growth lines, being closer to the posterior margin than to the anterior margin There is some variation in the degree of elongation of the shell in the earlier stages, some specimens being wider than the holotype and some narrower

DIMENSIONS Holotype length (not quite complete) 98 1 mm , height (not quite complete) 157 5 mm , thickness (both valves) 28 0 mm

REMARKS The change in direction of growth seems to be characteristic *Vulsella elongata* (von Schauroth) as figured by Oppenheim (1901*a*, p 148, fig 13), from the Priabonian of Lonigo, is narrower and straight *V granellensis* Oppenheim (1901*a*, p 150, fig 14), from the Priabonian of Mt Granella in Val di Bovo, while somewhat oblique ventrally, is distinctly wider

VULSELLA sp A

(Figure 35, plate 10)

MATERIAL *Rakhi Nala section* Upper Chocolate Clays (lower part, local zone 12) (FB F 1978, the holotype, Reg No L 79894), *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2539, *1*), *Kohat area* (*Panoba section*) Lower Kohat Shales (local subzone 4*a*) (FB F 2251, *4*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *15*+, FB F 2255, *8*)

DESCRIPTION Shell incomplete, partly broken, apparently transversely suboval, the direction of growth soon becoming at right angles to the original direction Umbonal region moderately strongly inflated, but later stages are considerably flatter Surface smooth except for scaly, lamellar growth lines 2 to 3 mm apart, these may, in part at least, be due to weathering

DIMENSIONS Holotype length (incomplete) 27 1 mm , height (incomplete) 18 8 mm

REMARKS The specimens are not sufficiently well preserved for precise comparison with other species The change in direction of growth and the lamellar, scaly growth lines appear to be characteristic

VULSELLA sp B

(Figures 36, 37, 38*a*, *b*, plate 10)

MATERIAL *Rakhi Nala section Pellatispira* Beds (local zone 15) (FB F 1980, the holotype, Reg No L 79895, and 9 fragmentary topotypes, Reg No L 79896–901, FB F 1981, *1*), *Zinda Pir section* White Marl Band (local zone 11) (FB F 2734, *1*), *Pellatispira* Beds (local zone 15) (FB F 2507, *1*, FB F 2737, *1*)

DESCRIPTION Shell very elongate in the direction of its height, straight in the young forms, tending to be slightly curved ventrally in larger specimens, apparently gaping umbonally, smooth, flattish to gently or moderately convex

Dimensions Holotype length 29 0 mm , height (incomplete) 55 2 mm Topotypes (1) length 30 1 mm , height (incomplete) 51 4 mm , (2) length 13 6 mm , height (nearly complete) 40·0 mm

Remarks The material is not sufficiently well preserved for precise comparison with other forms *Vulsella lignaria* Oppenheim (1903*a*, p 71, Pl 17, fig 4), from the Lower Mokattam of Egypt, is not so narrow, the form of the growth lines being different *V crispata* Fischer (1871, p 231, Pl 11, fig 2), from the Eocene of Egypt, has a spinose margin to one side of the umbonal region None of the other smooth forms figured by Oppenheim (loc cit) has an outline similar to this Rakhi Nala form *V grandicubitus* n sp is considerably larger and has a different outline even in the younger stages

Genus *EUPHENAX* Cox, 1931

(*Proc Malac Soc Lond* **19**, 177, Pl 20, figs 1–8, Pl 21, figs 1, 2, 4)

Type species *Pseudoheligmus* (?) *jamaicensis* Trechmann, Eocene, original designation

EUPHENAX JAMAICENSIS (Trechmann), 1923

References *Pseudoheligmus*? *jamaicensis* Trechmann, 1923 (p 358, Pl 18, figs 1–9)

Euphenax jamaicensis (Trechmann) Cox, 1931*b* (p 178, Pl 20, figs 1–8, Pl 21, figs 1, 2, 4), Cox, 1931*a* (pp 62, 28, 32, 34), Brown, 1931 (p 267), Cotter, 1933 (p 98), Cox, 1936 (pp 29, 7, Pl 3, figs 12, 13), Vokes, 1937 (pp 2, 3), Furon, 1941 (p 335), Trechmann, 1943 (p 78)

Material *Kohat area* (*Tarkhobi section*) Kohat Shales (probably lower part, local subzone 4*a*) (FB F 2183, 16 specimens, Reg No L 79902–7), *Kohat area* (*Panoba section*) Kaladhand Limestone (local subzone 4*a*) (FB F 2245, *1*, FB F 2254, *15*+, FB F 2255, *5*, FB F 2295, *15*+), Upper Kohat Shales (local subzone 4*a*)(FB F 2256, *15*+), *Kohat area* (*Shekhan Nala section*) Kaladhand Limestone (local subzone 4*a*) (FB F 2333, *3*, FB F 2334, *1*, FB F 2335, *1*, FB F 2336, *7*), Upper Kohat Shales (local subzone 4*a*) (FB F 2337, *3*, FB F 2341, *1*), *Kohat area* (*Sirki Paila*) Sirki Shale/Kohat Limestone (local subzone 4*d*) (FB F 2114, *1*) Accessory samples *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *15*+, FB F 2184, *4*)

Further distribution in Pakistan The species has been recorded by Cox (1931*a*) from the Kohat Shales of Kohat, and Bahadur Khel

Other records The type locality is the Yellow Limestone (Lutetian) of Jamaica (see Trechmann, 1923) The species has also been recorded by Cox (1936) from the Middle Eocene of Bahrein Island, and by Cox (1931*a*) from the Lutetian of Somaliland

Remarks The writer agrees with Dr L R Cox (verbal information) that *Euphenax coxi* Vokes (1937, p 2, fig 1), from the Lower Subathu (Khirthar) of a locality 21 miles north-west of Simla and 5 miles north-west of Arki, is probably synonymous with *Euphenax jamaicensis* (Trechmann), the latter species is known to be very variable, and the differences pointed out by Vokes may be due to individual variation, to mode of preservation, or a combination of these factors

Family PINNIDAE

Genus *PINNA* Linné, 1758

(*Syst Nat* 10th ed p 707)

Type species *Pinna rudis* Linné, Recent, Children, 1823

Synonyms The substitute names *Pinnarius* Duméril, 1806 (*Zool Analyt* p 340) and *Pinnula* Rafinesque, 1815 (*Anal de la Nature*, p 147) are absolute synonyms and have the same type species The invalid names *Chimaera* Poli, 1791 (*Test Sicil* 1, Introd p 31) *non* Linne, 1758 (*Pisces*)—the type species being given by Winckworth (1929, p 282) as *Pinna nobilis* Linné, Recent—and *Chimaeroderma* Poli, 1795 (*Test Sicil* 2, 253, 259) are also synonyms

Remarks Grant & Gale (1931, p 145) pointed out that the type species of *Pinna* Linné, 1758 should be *Pinna muricata* Linne, Recent = *Concha Pinna* Hasselquist by absolute tautonymy In the tenth edition of Linnaeus (1758), however, there are two misprints on p 707 under the heading of *Pinna muricata* First, the page number in Hasselquist (1757) is given as '447' instead of '448' and, secondly, the form referred to by Hasselquist is quoted as being '*Concha Pinna*' instead of '*Concha* (*Pinna*)' The word '*Pinna*' was not therefore used in a specific sense by Hasselquist, and is merely a colloquialism, consequently, Article 30 1(*d*) and Opinion 16 of the International Rules of Zoological Nomenclature do not apply The type species is therefore regarded as being *Pinna rudis* Linne, as designated by Children in 1823

PINNA PUNJABENSIS n sp

(Figures 39*a*, *b*, plate 11)

Material Ghazij Shales, south of Nila Kund, Dera Ghazi Khan District, Punjab, the holotype (Reg No L 77898) and 4 topotypes (Reg No L 77897, 77899, 77900, 77901), *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1845, *2*, FB F 1860, *2*), Shales with Alabaster (local zone 7) (FB F 1928, *7*, Reg No L 79809–10), *Pellatispira* Beds (local zone 15) (FB F 1992, *6*, FB F 1993, *1*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2732, *1*, FB F 2554, *2*)

Description Shell of moderate size, thin-shelled, strongly inflated when not crushed, quadrate in section, medially carinate, triangular in outline Umbos anterior, terminal Dorsal margin long, straight Ventral margin also straight, at an angle of about 30° to the dorsal margin Posterior end broken, apparently gaping Median carination sharply rounded on the holotype, appearing subangular and with a distinct longitudinal furrow on internal moulds That part of the surface dorsal to the carination carries 8 to 12 strong, distinct, longitudinal threads according to the size of the specimen, they are 2 to 2½ mm apart posteriorly on the holotype Ventrally to the median carination there are two types of ornament First, oblique folds rise upward from the ventral margin, gradually curving round to meet the median carination at an angle of about 30°, some of the internal moulds of young specimens give the false impression that these folds meet the carination almost at right angles On the adult shell these folds are as much as 3½ mm from crest to crest Secondly, there is a series of radial threads similar to, but somewhat less strong and less regular than, those on the dorsal part of the shell, these are stronger near the carination, and fade out ventrally They are at times even somewhat vermicular, and their spacing is about the same as or slightly less than that of those on the dorsal part of the shell There seems to have been a dorsal furrow in which the ligament was sunk, stretching about 25½ mm from the umbo on the holotype

Dimensions Holotype length (incomplete) 42 0 mm , height (incomplete) 22 2 mm , thickness (both valves—probably incomplete) 19 0 mm

Remarks The holotype has been chosen from Mr Pinfold's collection of specimens in the Natural History Museum since they are better preserved than those from the standard sections The valves are less sharply carinate than in *Pinna asakuraensis* Nagao (1928, p 31(21), Pl 8, figs 16, 18, 20–22), from the Kawamagiri Beds of Japan *P saccoi* V de Regny (1898, p 184, Pl 20, figs 11, 12), from the Priabonian of north Italy, is close to it in general appearance, but is more cuneiform and has rather less closely spaced and less regular ribs *P margaritacea* Lamarck as figured by Cossmann & Pissarro (1904*a*, Pl 39, fig 120–1), from the Bartonian of Ver and from the Lutetian of the Paris Basin, is more pointed anteriorly Specimens of the Paris Basin species that are kept in the Natural History Museum show that it is also less strongly convex and the concentric folds on the ventral portion of the shell rise up in a much sharper curve to meet the carination almost at right angles, a feature giving the shell a blunter appearance at its posterior end

PINNA SHEKHANENSIS n sp

(Figure 40, plate 11)

Material *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2369, the holotype, Reg No L 79908)

Description Shell of large size, the single specimen being slightly broken umbonally, where it was evidently moderately pointed, the dorsal margin is long and straight, and the posterior margin broadly rounded The valve is apparently a left valve, and is bluntly carinate along a line from the umbonal region to the postero-ventral corner Ornament ventral to the keel worn off, dorsal to the keel, the ornament consists of several broad, strong radial ribs, apparently having three finely crenulated threads in between them, with still finer threads in the intervals of these The primary ribs widen with age, forming on the posterior end folds of at least the same width as their intervals Distinction between primary ribs and those of other orders less well marked in the umbonal region

Dimensions Holotype length 117 0 mm (incomplete), height 72 5 mm , thickness (one valve) approximately 40 0 mm

Remarks The specimen is not very well preserved, but shows the ornament well in places *Pinna affinis* J Sowerby as figured by Wood (1861, p 55, Pl 10, fig 1), from the Eocene of Bognor, has no intercalary radial ornament, and the postero-ventral margin is apparently more acutely rounded The ornament and size of *P shekhanensis* appear to be characteristic

Superfamily ANOMIACEA

Family ANOMIIDAE

Genus *ANOMIA* Linné, 1758

(*Syst Nat* 10th ed p 700)

TYPE SPECIES *Anomia ephippium* Linné, Recent, Schmidt, 1818
SYNONYMS *Fenestella* Bolten, in Roding, 1798 (*Mus Bolt* 2, 193), Type species *Fenestella ephippium* Bolten, Recent = *Anomia ephippium* Linné)
Fenestrella Gray, 1847 (*Proc Zool Soc Lond* 15, 201) (*em*)

ANOMIA INTERRUPTA n sp

(Figures 41*a*,*b*,*c*, plate 11)

MATERIAL *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1920, *2*, FB F 1921, *2*, FB F 1922, the holotype, Reg No L 79909, and 1 topotype, Reg No L 79910, FB F 1925, *2*, FB F 1932, *2*, FB F 1933, *4*, FB F 1937, *1*, FB F 1944, *1*)

DESCRIPTION Shell of moderate size, strongly convex, suborbicular, or sometimes irregular if poorly preserved Umbo small, median Shell internally nacreous Ornament consisting of distinct, fine, rounded, raised radial threads, usually a little narrower than their intervals but occasionally a little wider, they are continuous for long distances, but on the postero-dorsal margin are often seen to stop and be continued *en echelon*

DIMENSIONS Holotype length 26 6 mm , height 24 2 mm , thickness (left valve only) 8 5 mm

REMARKS There is a slight possibility that Noetling's *Anomia densistriata* (1905, p 134)—a *nomen nudum*—may belong here, but it seems more likely to be *Pannomya blanfordiana* Cox *Anomia pakistanica* n sp has distinctly coarser and more interrupted radial ornament *A tenuistriata* Deshayes and its variety *libyca* Desio (1934, p 100, Pl 12, figs 8, 9), from the Eocene of north Africa, are similar but somewhat smaller, the more inflated variety *libyca* has more tumid umbos than *A interrupta*, whereas the species itself (fig 8) seems less inflated Dainelli's figures (1904, p 199, Pl 15, figs 2–4) of *A tenuistriata* Deshayes, from the Eocene of Dalmatia, are of a more oblique form than *A interrupta*, as is Frauscher's figure (1886, p 70, Pl 3, fig 10) of the same species from the Eocene of the northern Alps Cossmann's figures of Deshayes's species from the Eocene of Campbon and Bois-Gouet show a smaller form apparently with weaker ornament Cossmann & Pissarro's figures of Deshayes's species (1907–13, Pl 44, fig 136–1), from the Lutetian of Chaumont, while of the same size, may be somewhat less inflated A study of specimens of *A tenuistriata* in the Natural History Museum, however, shows that the essential difference between it and *A interrupta* is that the radial ornament consists of fine, incised radial striae separating flat ribbons, instead of distinct radial threads

ANOMIA PAKISTANICA n sp

(Figures 42*a*, *b*, plate 11)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2731, the holotype, Reg No L 79911)

Description The lateral and ventral margins are broken, but it can be seen from the growth lines and the general appearance that the shell was oval-suborbicular in outline and a little higher than wide The single specimen is a left valve, and is not very convex, the greatest convexity being in the umbonal region Umbo minute and pointed, situated just below the dorsal margin The broken margin shows that the shell was internally nacreous Ornament distinctive, consisting of irregularly oval or elongate, prominent ridges, regularly arched in transverse section, and arranged in an irregular radial fashion, the appearance is therefore somewhat vermicular

Dimensions Holotype length (not quite complete) 18 2 mm , height 19 8 mm , thickness (left valve only) about 3 2 mm

Remarks There does not appear to be any closely related Eogene species The relatively coarse and prominent ornament is distinctive The ornament is too fine for a *Parinomya*

Genus *PARINOMYA* Olsson, 1928

(*Bull Amer Paleont* **14**, no 52, p 19(65))

Type species *Carolia* (*Parinomya*) *parinensis* Olsson, Eocene, original designation (and monotypy)

PARINOMYA BLANFORDIANA Cox, 1938

References *Parinomya blanfordiana* Cox, 1938*b* (p 165, figs 3*a*, *b*, *c*)

Doubtful references *Anomia densistriata* Noetling, 1905 (p 134) (*nomen nudum*)

Material *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1920, several specimens, FB F. 1922, *2*, FB F 1925, *4*, FB F 1927, *2*, FB F 1928, *10*+, FB F 1929, *2*, FB F 1930, several specimens, FB F 1931, several specimens, FB F 1932, *2*, FB F 1933, *4*, FB F 1935, *2*, FB F 1938, *6*, Reg No L 79913–8, FB F 1939, *1*, FB F 1940, *1*, FB F 1942, several specimens, FB F 1943, *1*, FB F 1951, *1*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *7*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *15*+), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *1*, FB F 2294, *6*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2291, *1*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *2*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *1*, FB F 2296, *3*), *Kohat area* (*Shekhan Nala section*) Middle Shekhan Limestone (local subzone 3*a*) (FB F 2318, *1*), Kaladhand Limestone (local subzone 4*a*) (FB F 2336, *7*), Upper Kohat Shales (local subzone 4*a*) (FB F 2337, *15*+)

Accessory samples *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *15*+, FB F 2184, *15*+)

Further distribution in Pakistan ?Uppermost Laki of the Dharan Pass (Cox), Ghazij Shales (Upper Laki, Ypresian), south of Nila Kund, Dera Ghazi Khan District (Cox), low horizon in Kohat Shales (Lower Khirthar, Lutetian) of Kohat, North-West

Frontier Province (Cox), probably from the Ghazij Shales of Baluchistan and the Dharan anticline (Noetling)

Remarks The holotype was recorded by Cox (p 166) from the Lower Khirthar (Lutetian) of the Dharan Pass, Laki, Sind, but an examination of the Bara Dome section of the Laki Range has indicated that the specimens are more likely to have come from the shales of Upper Laki age immediately underlying the Khirthar limestones and overlying the Laki Limestone The type occurrence is therefore almost certainly of uppermost Laki age Noetling's records of *Anomia densistriata* (a *nomen nudum*) from the Ghazij Shales of Baluchistan and the Dharan anticline almost certainly belong here too, although there is a slight possibility that the form might be *A interrupta*

PARINOMYA PINFOLDI Cox, 1938

References *Parinomya pinfoldi* Cox, 1938*b* (pars) (p 164, Pl 6, figs 1*a*, *b*, *c*, Pl 7, fig 1 *non* Pl 6, fig 2 = *Parinomya coxi* n sp)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 11) (FB F 1969, *2*, Reg No L 79919–20), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2559, *2*, FB F 2557, *2*, FB F 2733, *2*, FB F 2556, *4*, FB F 2555, *10*+, FB F 2565, *2*, FB F 2564, *2*, FB F 2731, *2*, FB F 2552, *10*+, FB F 2550, *10*+)

Further distribution in Pakistan In shales between the Habib Rahi and Pir Koh Limestones (Lower Khirthar, Lutetian) from (*a*) Mile 56, Moghul Koh Road, Dera Ismail Khan District (type locality), (*b*) Khalgari Nala, Dera Ghazi Khan District, and (*c*) Khaura Sai, north of Khosa, Dera Ghazi Khan District (all recorded by Cox) These horizons are in the Lower Chocolate Clays

Remarks The specimen figured by Cox on Pl 6, fig 2, has a considerably more inflated left valve and much finer ornament than on even the most finely ornamented *Parinomya pinfoldi* the writer has seen, specimens in the Natural History Museum suggest that the plug in the right valve is also larger and more elongate than in *P pinfoldi*

Superfamily PECTINACEA

Family PECTINIDAE

Subfamily PECTININAE

Genus *CHLAMYS* Bolten, in Roding, 1798

(*Mus Bolt* pt 2, p 161)

Type species *Chlamys cinnabarina* Bolten, Recent = *Pecten islandicus* Muller, Herrmannsen, 1847

CHLAMYS WYNNEI Cox, 1931

References *Chlamys wynnei* Cox, 1931*a* (pars) (pp. 66, 28, 29, 34, Pl 3, figs. 9, 10, ?*non* fig 11 = *Chlamys* sp), Cotter, 1933 (p 97)

Pecten favrei d'Archiac, Wvnne, 1868 (p 30), Blanford, 1869 (p 208)

P favri d'Archiac, Wynne, 1872 (p 251)

P bouei d'Archiac, Wynne, 1872 (p 248)

P bouei d'Archiac & Haime, Noetling, 1905 (p 172)

Pecten sp L M Davies, 1925 (p 210), L M Davies, 1926*b* (p 208)

Further references probably to be included *Pecten bouei*? d'Archiac, T Oldham, 1875 (p 179)

Material *Rakhi Nala section* Upper Chocolate Clays (local zone 12) (FB F 1973, *1*, Reg No L 79921, FB F 1976, *1*, FB F 1979, *2*, FB F 2751, *1*), *Zinda Pir section* White Marl Band (local zone 11) (FB F 2548, *4*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2533, *2*, FB F 2531, *6*), *Kohat area* (*Panoba section*) Nummulite Shales (local subzone 4*b*) (FB F 2267, *1*), Kohat Limestone (local subzone 4*b*) (FB F 2271, *1*, FB F 2272, *1*, FB F 2273, *2*), *Kohat area* (*Shekhan Nala section*) Upper Kohat Shales (local subzone 4*a*) (FB F 2342, *3*), Nummulite Shales (local subzone 4*b*) (FB F 2346, *2*, FB F 2347, *1*, FB F 2348, *1*, FB F 2349, *2*, FB F 2352, *1*), Kohat Limestone (local subzone 4*c*) (FB F 2357, *2*, FB F 2358, *2*), *Kohat area* (*Sirki Paila*) Kohat Limestone (local subzone 4*d*) (FB F 2113, *2*), Sirki Shale (local subzone 4*d*) (FB F 2115, *15*+, FB F 2107, *15*+, FB F 2108, *15*+, FB F 2109, *15*+, FB F 2110, *15*+, FB F 2111, *7*, FB F 2112, *15*+), Sirki Shale/Kohat Limestone (local subzone 4*d*) (FB F 2114, *5*, Reg No L 79222–6)

Further distribution in India and Pakistan Khirthar of Bhodan, Surat (Cox), of Ukree, Cutch (Cox), of Baboa Hill, Cutch (Cox), of Panundrow, Cutch (Cox), of Baluchistan (Noetling) Nummulite Shales of Kohat (L M Davies and Cotter), of Chharat—the holotype (Cox)—and of Saidgi (L M Davies, 1926*b*) Kohat Shales of Kohat (Cox), and of Harnai (Cox) Possibly also from the Prang Limestone (Khirthar) of the Khasi Hills, Assam (Oldham)

Remarks As pointed out by Cox there is some similarity between this species and immature or small specimens of *Chlamys senatoria* (Gmelin) which is common in the Lower Miocene Gaj beds and ranges up to Recent The matrix of the specimen illustrated by Cox in his fig 11 is quite unlike any that the writer has seen while working on collections from a very large number of fossil beds from the Eocene of various parts of the Salt Range The matrix of this specimen has been sliced, and the rock slides, while showing no trace of larger Foraminifera (which would be unusual for a rock of this type), show some resemblance to slides of brown algal limestones the writer has had made from material from the Gaj of Sind Cox's specimen is believed to have come from the Chichalee Pass of the Salt Range, and would therefore be of Laki age There are no other Laki records, and the species has not yet been found in the Laki collections of the Burmah Oil Co Ltd , and consequently the writer suggests that the specimen has become inadvertently misplaced in old collections In view of the several doubts involved, it seems better to neglect this record until it can be substantiated

CHLAMYS SORIENSIS n sp

(Figure 23, plate 9)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2535, the holotype, Reg No L 79927)

Description The single broken specimen is probably a left valve The dorsal region has been lost, but what remains shows that the shell was not very large, obliquely oval, the outline being strongly convex and rather asymmetrical ventrally Shell somewhat crushed, and appearing rather flat Ornament beautifully preserved, consisting of sharp, V-shaped ribs with intervals one and a half to two times as wide as the ribs There are 27 ribs altogether on what remains of the shell, two of the ribs on what is assumed to be the antero-ventral portion of the shell are strong intercalaries Intervals between ribs ornamented with minutely serrated, very fine, but distinct, concentric threads of which there are 8 to 12 in ¾ mm

DIMENSIONS Holotype length 13 8 mm , height (incomplete) 10 5 mm

REMARKS Although there is only one broken specimen available, the ornament is so beautifully preserved that it seems worth naming It is somewhat like the left valve of *Pecten arcuatus* (Brocchi) as figured by Cossmann (1922*a*, p 166, Pl 10, figs 4–8), from the Rupelian of le Phare (Biarritz), but distinctly higher and more oblique, with a decidedly more convex ventral margin, and with somewhat thinner and sharper ribs including at least 2 strong intercalaries The ventral margin is more oblique and convex and the ribs finer than in *P sylvestrei-sacyi* Cossmann (1919, p 138, Pl 4, figs 7–9), from the Oligocene of Rennes Compared with *P mitis* Deshayes (1830, p 306, Pl 44, figs 13–15)—also referred to as *Chlamys mitis* Deshayes by Cossmann & Pissarro (1904*a*, Pl 40, fig 131–7)—from the Lutetian of Parnes, the ventral margin is more obliquely convex and the ribs are a little sharper and have wider intervals Compared with *C vapincana* Boussac (1911*a*, p 157, Pl 7, fig 15), from the Bartonian (Lower Priabonian) of Faudon, the ornament is less coarse, the ribs more uniform in size, and the ventral margin more sharply and obliquely convex *C thunensis* (Mayer-Eymar) as figured by Boussac (1911*a*, p 156, Pl 7, figs 20, 21), from the Auversian of Ralligholz, has similar fine ornament, but the ribs are less uniform in size and are occasionally bifurcate or double

CHLAMYS PAKISTANICA n sp

(Figure 43, plate 11)

MATERIAL *Zinda Pir section Pellatispira* Beds (local zone 15) (FB F 2737, the holotype, Reg No L 79928, and 2 topotypes, Reg No L 79929–30)

DESCRIPTION Shell of moderate size, orbicular-chlamydiform, inflation slight, right valve almost flat Anterior ear of right valve with a byssal sinus, it is ornamented with a double thread dorsally, followed by 4 subequal, sharp threads and then a still finer one, all threads being crossed by scaly concentric growth lines which are more irregular and more widely spaced than over the rest of the shell Anterior ear of left valve, apart from having no byssal notch, similarly ornamented Concentric ornament on both anterior and posterior ears extending on to their dorsal edges, giving them a serrated appearance Surface of valves not completely preserved, but there were probably a little more than 30 strong, flattened radial ribs which are about twice as wide as their intervals in the young stages, but become three or four times as wide as their intervals in the adult shell These ribs are crossed by very regular, slightly wavy, sharp, distinct, concentric, scaly growth lines numbering 4 in ¾ mm ventrally on the holotype, in the umbonal region the scaly growth lines are more closely spaced, there being about 8 in ¾ mm Concentric ornament apparently crossing the intervals between the ribs, but not so prominent there Valve margins internally fluted

DIMENSIONS Holotype length (incomplete) 19 3 mm , height 29 1 mm A topotype length 13 8 mm , height 15 0 mm

REMARKS This form has more numerous ribs with narrower intervals, and is less oblique than *Chlamys bormidiana* Rovereto (1900, p 59, Pl 3, fig 1), from the Lower Tongrian of Pareto It is a little smaller, less high, and has flatter ribs compared with *Pecten eocaenicus* Mayer-Eymar as figured by Frauscher (1886, p 96, Pl 12, fig 13), from the Lower Eocene (Londinian) of Sentis, Switzerland The intervals between the ribs are narrower and the ventral margin a little more convex than in *Chlamys morgani* Cossmann & Pissarro (1903, p 16, Pl 1, fig 21), from the Eocene of Hauteville (Cotentin) *C pradellensis* Doncieux (1911, p 43, Pl 7, figs 2*a*, 2*b*, 3), from the Lower Lutetian south-west of Fontcouverte, is rather broader, does not attain such a large size, and has relatively narrower ribs

Subfamily AMUSIINAE

Genus *AMUSIUM* Bolten, in Roding, 1798

(*Mus Bolt* 1st ed , pt 2, p 165)

TYPE SPECIES *Ostrea pleuronectes* Linné, Recent, Dall, 1886

SYNONYMS *Amussium* (Rhumphius, 1711) Agassiz, 1846 (*Nomencl zool Index*, p 19) (*em*) *Pleuronectia* Swainson, 1840 (*Treat Malacol* p 388), type species *P laevigata* Swainson, Recent, monotypy

Subgenus *PSEUDENTOLIUM* Cox, 1948

(*Abh Schweiz pal Ges* **66**, 63)

TYPE SPECIES *Pecten corneus* J Sowerby, Eocene-Oligocene, original designation

AMUSIUM (*PSEUDENTOLIUM*) *CORNEUM* (J Sowerby), 1818

REFERENCES *Pecten corneus* J Sowerby, 1818 (3, 1, Pl 204, figs 1, 2), J Sowerby, 1838 (p 252, Pl 204), Nyst, 1843 (Pl 23, figs 1*a*,*b*), Morris, 1843 (p 114), J Sowerby, 1844 (p 299), Nyst, 1845 (p 299), Prestwich, 1846*a* (p 230), Prestwich, 1846*b* (pp 358, 370), Dixon, 1850 (pp 24, 94, Pl 4, fig 6), d'Orbigny, 1850 (p 393), Le Hon, in Lyell, 1852 (p 353), Morris, 1854 (p 178), Prestwich, 1857 (p 98), Wood, 1861 (p 39, Pl 9, figs 7*b*,*c*), Guembel, 1861 (p 608), Le Hon, 1862 (p 826), Schafhautl, 1863 (p 151, Pl 33, fig 6), von Schauroth, 1865 (p 99), von Koenen, 1865 (pp 519, 531, 465), d'Archaic, in Tchihatcheff, 1866 (p 145), Fuchs, 1867 (p 194), Quenstedt, 1867 (p 603), Wynne, 1868 (p 30), Nyst, in Dewalque, 1868 (p 406), Blanford, 1869 (p 208), von Koenen, 1869 (pp 590, 594, 597), Fuchs, 1869 (pp 83, 92), von Hantken, 1872 (p 107), Whitaker, 1872 (p 593), Lefèvre & G Vincent, 1872 (p. 28), Hofmann, 1872 (p 197), G Vincent & Lefèvre, 1872 (p 72), G Vincent, 1873*a* (p 13, Pl 1, fig 4), Lefèvre, 1874 (p 73, Pl 4), Crosse, 1875 (p 270), Meunier, 1875 (p 152), K Mayer-Eymar, 1877 (p 77), Dixon, 1878 (p 233, Pl 4, fig 6), Moesch, 1878 (p 8), G Vincent & Rutot, 1879 (p 143), Balzer, 1880 (p 60), G Vincent & Rutot, in Mourlon, 1881 (pp. 155, 163, 177, 187, 201), Zittel, 1883 (p 125), G Vincent & Rutot, 1883 (p 198), De Limburg, 1883 (p 97), Raeymaekers & van Ertborn, 1883 (p 27), Frauscher, 1886 (p 95), G Vincent, 1886*a* (p 12), G Vincent, 1886*b* (p 59), Cossmann, 1887 (p 178), C Mayer-Eymar, 1887 (p 90), Guembel, 1888 (p 893, fig 6, 894, 921), Noetling, 1888 (p 33, Pl 3, figs 9–11*a*), C Mayer-Eymar, 1893 (p 27), Couturieux, 1893 (p XVII), Sokolow, 1893 (pp 137, etc), von Koenen, 1893 (p 1020, Pl 67, figs 1–3), Koch, 1894 (pp 297, 302, 312, 315, 321, 327, 348), von Koenen, 1894 (p 1377), E Vincent, 1897 (p X), Radkewitsch, 1900 (pp 343, 350, 357, 358), Oppenheim, 1901*a* (p 313), Deninger, 1901 (p 240), Cossmann, 1901*a* (pp 22, 23), Oppenheim, 1903*b* (p 211), Dreger, 1903 (pp 259, 281, Pl 12, fig 2), Sokolow, 1905 (pp 43, 77, Pl 9, fig 3, Pl 10, figs 1*a*,*b*), Fabiani, 1908 (p 52), Taeger, 1908 (pp 93, 94, 97), Fabiani, 1915 (pp 5, 52, 66, 70), Dollfus, 1918 (p 101), Oppenheim, 1922 (p 99), Schlosser, 1922 (pp 279, 287, 291), Dukooizen, 1924 (pp 10, 37), Rogala, 1925 (p 938), Schlosser, 1925*b* (pp 45, 51, 56), Vialov, 1934*a* (p 144), Tomor-Thirring, 1935 (p 7), Léonov, 1936 (pp 300, 304, 307, 309, 312, 313), Loss, 1940 (p 6), Albrecht & Valk, 1943 (pp 147, 150, 151, 153), Illies, 1949 (p 16)

'*Pecten*' *corneus* J Sowerby, Wrigley, 1940 (pp 236, 241)

P (*Cornelia*) *corneus* J Sowerby, C Mayer-Eymar, 1887 (p 124)

P (*Entolium*) *corneus* J Sowerby, Oppenheim, 1900*a* (p 136, text-fig 12), E Philippi, 1900 (p 81, text-fig 4), Deninger, 1901 (p 226), Fabiani, 1908 (p 185), Schlosser, 1922 (p 261), Schlosser, 1925*b* (p 17), Loss, 1940 (pp 36, 70)

P (*Entolium*) *corneum* J Sowerby, E Noszky, 1926 (p 301)

P (*Pseudamusium*) *corneus* J Sowerby, Lukovitch, 1921

P (*Pseudamussium*) *corneum* J Sowerby, Dukovnu, 1924 (p 37)

P (*Amussium*) *corneum* J Sowerby, Rogala, 1925 (p 936)

P (*Amussium*) *corneus* J Sowerby, Leriche, 1939*a* (p B 556)

P (*Camptonectes*) *corneus* J Sowerby, Albrecht & Valk, 1943 (p 117, Pl 10, fig 356)

Pseud-amusium corneus (J Sowerby), Newton, 1891 (p 7)

Pseudamussium corneum (J Sowerby), Sacco, 1897*b* (p 51), Verrill, 1897 (p 61), de Alessandri, 1901 (p 100), Sacco, 1904 (p 145), Cossmann, 1922*a* (p 181, Pl 11, fig 26), Gripp, 1925 (p 135), Slodkewitsch, 1928 (pp 561, 570), Meffert, 1931*b* (pp 1150, 1154, 1155), Slodkewitsch, 1932 (pp 42, 65, 11, Pl 3, fig 3), Korobkov, 1935 (pp 126, 127, 128), Vialov & Korobkov, 1939 (pp 38, 43, 34, Pl 1, figs 1, 2)

Pseudamusium corneum (J Sowerby), Stoliczka, 1871 (p 426), Jackson, 1926 (p 352)

Pseudamussium corneum (J Sowerby), Ruzin, 1935 (p 38)

Chlamys cornea (J Sowerby), Couturieux, 1896 (p xxvi), G Vincent & Couturieux, 1896 (p xlii)

Amussium corneum (J Sowerby), de Gregorio, 1898 (pp 20–22), Ugolini, 1899 (p 187), Boussac, 1911*b* (pp 29, 81), Boussac, 1911*a* (pp 153, 404, Pl 6, fig 19), Fabiani, 1915 (pp 258, 265), Dalloni, 1917 (pp 105, 110), Stefanini, 1921*a* (pp 119, 131), Deperet & Roman, 1928 (p 185), Wrigley, 1929*b* (p 103), Burton, 1933 (p 153), Wrigley, 1934 (p 7), Davis, 1936 (p 337), Curry, 1942 (pp 92, 96), Roger, 1944 (pp 6, 48, 53), Stchepinsky, 1945 (pp 137, 147)

Amusium corneum (J Sowerby), Glibert, 1936 (p 216)

A (*Eburneopecten*) *corneum* (J Sowerby), Glibert, 1936 (pp 52, 206, 211, Pl 2, fig 2)

A (*Entolium*) *corneum* (J Sowerby), Burch, 1937 (p 187)

Entolium corneum (J Sowerby), von Teppner, 1922 (p 89)

Pecten semperi Deshayes, 1861 (p 73)

P corneus J Sowerby var *corneolus* Wood, 1861 (p, 39, Pl 9, fig 7*a*)

Chlamys (*Pseudamussium*) *corneola* (Wood), Cossmann, 1887 (pars) (p 178), Harris & Burrows, 1891 (p 75)

Pecten bellardii C Mayer-Eymar, 1869 (pp 288–289), Kaufmann, 1872 (pp 82, 109, 533, Pl 6, fig 1)

Pseudamussium bellardii (C Mayer-Eymar), Sacco, 1897*b* (p 52)

Pecten tunetanus Locard, 1889 (p 50, Pl 10, fig 1)

Pseudamussium tunetanum (Locard), Sacco, 1897*b* (p 52)

P corneum (J Sowerby) mut *tunetanum* (Locard), Flandrin, 1938 (pp 130, 145, 148, fig 25)

P tournoueri Cossmann, 1922*a* (p 182, Pl 10, figs 42, 43), Schnaebele, 1948 (p 88)

Pecten cf *corneum* J Sowerby, Athanasiu, 1899 (pp 257, 264)

Pecten (*Entolium*) cf *corneus* J Sowerby, Vogl, 1912 (p 91)

Pecten aff *palmatus* Lamarck, Deninger, 1901 (p 226)

Amusium (*Pseudentolium*) *corneum* (J Sowerby), Cox, 1949 (p 63)

Camptonectes corneum (J Sowerby), Gillet, 1949 (pp 57, 72, Pl 4, fig 7)

INCORRECT REFERENCES *Pecten corneus* J de C Sowerby, Cya, 1883 (p 58), C Mayer-Eymar, 1893 (p 27)

MATERIAL *Rakhi Nala section* White Marl Band (local zone 11) (FB F 1964, *1*, Reg No L 79931), Upper Chocolate Clays (lower part, local zone 12) (FB F 1973, *2*, FB F 2096, *6*, FB F 1975, *1*), Upper Chocolate Clays (upper part, local zone 13) (FB F 1986, *10*+, FB F 1987, *1*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2758, *10*+), *Pellatispira* Beds (local zone 15) (FB F 1997, *1*), *Zindar Pir section* White Marl Band (local zone 11) (FB F 2548, *1*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, *10*+, FB F 2536, *2*, FB F 2537, *2*, FB F 2529, *1*, FB F 2522, *2*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2516, *10*+, FB F 2513, *1*, FB F 2738, *10*+), *Pellatispira* Beds (local zone 15) (FB F 2507, *1*)

FURTHER DISTRIBUTION IN INDIA Khirthar of Bhodan, Surat (Wynne, 1868, Blanford, 1869)

FURTHER DISTRIBUTION This well-known species has a very wide distribution and has been recorded from numerous localities It has been recorded from the Palaeocene of Russia, the Lower Eocene of Germany, the London Clay of England, the Middle Eocene of Asia Minor, Russia, Belgium, Switzerland, France, Italy and England, the Auversian of the Alps, the Barton Beds of England, the Wemmel Sands (Bartonian) of Belgium, the Bartonian of the Aral Sea region, Switzerland and Holland, the Upper Eocene of the Balkans, Hungary, the Bavarian Alps and Egypt, the Eocene of Russia, the northern Alps, the Crimea, the Tyrol, France and the Carpathians, the Priabonian of France, Italy, Hungary and Southern Dagestan, the Lower Oligocene of the Bavarian Alps, Russia and Belgium, the Lower Ligurian of Switzerland, the Rupelian of France, the Chattian of Hungary, the Oligocene of Cyrenaica, the Balkans, Algeria, Germany, France, Lower Alsace and Haring, the Lower Tertiary of Austria and Russia, and the Schio Beds of Dego The above is merely a summary of the published records C Mayer-Eymar's (1893) record from the Aquitanian Schio Beds of Dego is the highest stratigraphical horizon from which the species has been recorded, since it is the only Miocene record, and since Mayer-Eymar did not illustrate his material, the record might be regarded as somewhat doubtful The lowest record seems to be that of Slodkewitsch (1928) from the Palaeocene of the Donetz Basin Wrigley (1940), Davis (1936) and Newton (1891) have recorded the species from the London Clay of the London Basin

Remarks *Pecten solea* Deshayes, which was at one time by some authors placed in synonymy with *Amusium* (*Pseudentolium*) *corneum*, has a distinct notch beneath the right anterior ear The forms referred to as *Chlamys* (*Pseudamussium*) *corneola* (Wood) by Cossmann (1887, p 178 (pars)), and figured as *C* (*P*) *arneola* (Wood) by Cossmann (1887, Pl 8, figs 26, 31), from the Cuisian of Cuise, as well as those forms referred to as *Pecten corneolus* Wood by Cossmann (1901*a*, p 23), from the Eocene of Liancourt, and figured as *Chlamys* (*Pseudamussium*) *corneola* (Wood) by Cossmann & Pissarro (1907–13, Pl 63, fig 131–3), from the Cuisian of Cuise, and by Cossmann (1913, p 103, Pl 1, fig 131–3), from the Cuisian of Cuise, also have a distinct notch beneath the right anterior ear and belong to a different species if not to a different genus Mallada's record (1883, p 58) of *Pecten corneus* J Sowerby, from the Neogene of Spain, may also be regarded as incorrect Specimens in the British Museum of Natural History, from various localities in the London and Hampshire Basins, show that *P corneus* J Sowerby var *corneolus* Wood is merely an immature variant of *Amusium* (*Pseudentolium*) *corneum*

Deperet & Roman (1928) refer the group of *Amussium corneum* to *Entolium* Meek and *Pseudamussium* Sacco *non* Klein On the other hand, Cox (1949) places the subgenus *Pseudentolium* under the genus *Amusium* While it is true that neither *Entolium* nor *Pseudentolium* possess the numerous internal ribs of *Amusium*, the ears of the forms placed in the first two groups are very similar Since considerable importance is attached to the characters of the ears in the Pectinidae, the writer agrees with Cox that it is better to regard *Pseudentolium* as a subgenus of *Amusium* rather than of *Entolium*

Subgenus *ENTOLIOPSIS* n subg

Type species *Amusium* (*Entoliopsis*) *uniradiatum* n sp , Lower Eocene

Subgeneric characters Like *Pseudentolium*, but with a distinct raised ridge internally on the anterior part of the shell, radial in disposition, reaching neither the ventral margin nor the umbonal region, gradually increasing in width in a ventral direction, present on both left and right valves, also with one fine raised ridge internally limiting both ears ventrally on the right valve, and two closely spaced but distinct ones, separated by a groove, disposed similarly beneath each ear on the left valve Shell small

AMUSIUM (*ENTOLIOPSIS*) *UNIRADIATUM* n sp

(Figures 44*a*,*b*,*c*, 45*a*,*b*,*c*,*d*, plate 11)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 4) (FB F 1843, *10*+, FB F 1844, *10*+, FB F 1845, *10*+ , FB F 1846, *2*, FB F 1847, *2*, FB F 1848, *4*, FB F 1849, *10*+, FB F 1850, the holotype, Reg No L 79932, and *10*+ topotypes, Reg No L 79933–8, FB F 1851, *1*, FB F. 1854, *6*, FB F 2022, *10+*, FB. F 1855, *2*; FB F 1859, *4*, FB F 1860, *10+*, FB F 1867, *4*, FB F 1868, *10+*, FB F 1869, *10+*) Green and Nodular Shales (local zone 5) (FB F 1873, *1*), *Zinda Pir section* Ghazij Shales (local subzone 3*a*) (FB F 2681, *2*)

Description Shell small, subequivalve, externally smooth, inflation slight, suborbicular in outline except for the straight dorsal margin, subequilateral Valve margins internally smooth, but the internal surface shows radial lines of reflected light under certain conditions of illumination The single elongate raised radial ridge internally as described above Ears triangular Right anterior ear large, not notched, its anterior margin slightly concave and sloping upward very slightly toward the umbo Right posterior ear smaller, more obliquely triangular Left anterior ear like the right anterior ear, but its anterior margin slightly indented below Left posterior ear a little smaller, apparently less obliquely triangular than the right posterior ear Ears of left valve internally with one pair of raised crura close to the dorsal margin, and a distinct double pair of long raised ridges bordering the ventral margins of each ear where they meet the body cavity Hinge area of right valve similar, except that the more ventrally disposed ridges are single, not in pairs Resilifer small and triangular

Dimensions Holotype (left valve) length 4 9 mm , height 4 9 mm , thickness 0 75 mm A topotype (right valve) length 5 5 mm , height 5 1 mm , thickness 0 75 mm or slightly more

Remarks Neither *Pecten cossmanni* von Koenen (1893, p 1029, Pl 67, figs 16–20), from the Lower Oligocene of north Germany, nor *P hauchecornei* von Koenen as figured by Speyer (1884, Pl 27, figs 3, 4) possess the internal rib, the former species is higher and has differently shaped and broader ears, while the latter species is a little smaller and has larger ears

Family Spondylidae

Genus *SPONDYLUS* Linne, 1758

(*Syst Nat* 10th ed p 690)

Type species *Spondylus gaederopus* Linné, Recent, Children, 1823

Synonyms *Dianchora* J Sowerby, 1815 (*Min Conch* 1, 183), Type species if not already selected, should be chosen from *D striata* J Sowerby, Cretaceous and *D lata*, J Sowerby, Cretaceous

Podopsis Lamarck, 1819 (*An s vert* 6, pt 1, p 194), Type species if not already selected, should be chosen from *P truncata* Lamarck, Cretaceous and *P gryphoides* Lamarck, Cretaceous

Pachytos Defrance, 1824 (*Tabl Corps foss* p 109) (*nomen nudum*)

Pachytos Defrance, 1825 (*Dict Sci Nat* 37, 207), Type species if not already selected, should be chosen from *P striatus* Defrance, Cretaceous (=*Spondylus striatus* (J Sowerby)) and *P spinosus* Defrance, Cretaceous—the third species mentioned by Defrance (*P hoperi* Defrance) belongs to the Limidae and was named *Plagiostoma hoperi* Mantell

Pachytes Hoeninghaus, 1830 (*Jahrb Min* 1830, p 473) (error)

SPONDYLUS PERHORRIDUS Oppenheim, 1903

References *Spondylus perhorridus* Oppenheim, 1903*a* (p 66, Pl 3, fig 3), Cuvillier, 1930 (p 163), Cox, 1931*a* (pp 67, 28, 34, Pl 2, figs 8*a*,*b*), Cotter, 1933 (p 98)

Material *Kohat area* (*Gada Khel*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2102,*1*, Reg No L 79939)

Further distribution in Pakistan Kohat Shales of Kohat

Other records Lower Mokattam (Middle Eocene) of Egypt, the type locality (Oppenheim, 1903*a*, Cuvillier, 1930)

SPONDYLYS RADULA Lamarck, 1806

References *Spondylus radula* Lamarck, 1806*b* (p 351), Lamarck, 1810 (p 375, Pl 23, fig 5), Bronn, 1824 (p 52, Pl 6, fig 9), Deshayes, 1830 (p 320, Pl 46, figs 1–5), d'Archiac, 1846 (pp 186, 191), Bronn, 1848*b* (p 1189), Bellardi, 1852 (pp 260, 295), Deshayes, 1861 (p 90), Fuchs, 1869 (pp 87, 92, Pl 5, figs 1, 2), Fuchs, 1870 (p 142), A von Pavay, 1874 (pp 364, 413), von Hantken, 1875 (pp 354, 359), Vieillard & Dollfus, 1875 (p 100), K Mayer-Eymar, 1877 (p 77), Mallada, 1878 (pp 320, 325, 407), Mallada, 1882 (Pl 10, fig 7), Zittel, 1883 (p 115), Cossmann, 1887 (pp 188, 192), C Mayer-Eymar, 1887 (p 89), Harris & Burrows, 1891 (p 76), Mallada, 1892 (p 200), Sokolow, 1893 (pp 154, 177, 297, 322), Oppenheim, 1894 (p 445), Koch, 1894 (pp 227, 229, 243, 286, 297, 312), Vinassa de Regny, 1896*a* (pp 241, 228), Oppenheim, 1901*a* (p 137, Pl 12, fig 13), Cossmann & Pissarro, 1903 (p 14, Pl 1, figs 11, 12), Oppenheim, 1903*a* (p 62), Cossmann & Pissarro, 1904*a* (Pl 41, fig 134–1), Cossmann, 1904 (p 154, Pl 2, fig 5), Fabiani, 1908 (pp 181, 67, Pl 4, fig 14), Boussac, 1911*a* (pp 172, 406, Pl 8, fig 18), Vogl, 1912 (pp 90, 109), Dainelli, 1915 (pp 428, 77, 128, Pl 48, fig 21), Fabiani, 1915 (pp 258, 266), Vasseur, 1917 (Pl 18, fig 22), Cossmann, 1921*c* (p 119), Cossmann, 1921*b* (p 119), Dukooizen, 1924 (p 13), Schlosser, 1925*a* (pp 42, 161, 175, 195, 196), Abrard, 1925*a* (pp 94, 101, 109, 135), Gočev, 1926 (p 88), Gočev, 1929 (pp 86, 104), Cuvillier, 1930 (pp 56, 81), Cox, 1931*a* (pp 68, 28, 32, 34, 35, Pl 3, figs 23*a*,*b*), Brown, 1931 (p 267), Slodkewitsch, 1932 (pp 43, 65, Pl 3, fig 9), Gočev, 1933*a* (pp 35, 72, 8, 63, Pl 2, fig 5), Korobkov, 1935 (pp 126, 127, 128), Cox, 1936 (pp 31, 7, Pl 3, fig 10), Léonov, 1936 (p 307), Loss, 1940 (pp 31, 69, 72, Pl 2, fig 6), Furon, 1941 (p 335), Furon & Soyer, 1947 (p 101), Belmustakov, 1949 (pp 40, 53)

S radula Lamarck var Sokolow, 1905 (pp 46, 79, Pl 12, figs 8*a*,*b*, 9, 10)

S asperulus Munster, Goldfuss, 1836 (p 99, Pl 106, figs 9*a–d*), Bronn, 1848*b* (p 1188), d'Archiac, 1850*a* (pp 437, 454), Sismonda, 1852 (p 324), Bellardi, 1852 (pp 261, 295), Guembel, 1861 (p 622), Schafhautl, 1863 (p 147, Pl 33, figs 7, 8), Stukenberg, 1873 (pp 249, 154), Mallada, 1883 (p 55), Cya, 1883 (p 55), Oppenheim, 1901*b* (p 233), Fabiani, 1908 (p 182, Pl 4, fig 15), Dainelli, 1915 (pp 429, 77, 98, 128, Pl 48, fig 22), Loss, 1940 (pp 30, 7, 69, 72, 73, 76, 77, Pl 2, fig 5)

S aperulus Munster, Stukenberg, 1873 (p 263)

S gibbosus d'Orbigny, Schafhautl, 1863 (p 147, Pl 65, figs 12, 14)

S astralagus Schafhautl, 1863 (p 148, Pl 65*b*, fig 13)

Spondylus sp ? Taramelli, 1870 (p 44)

S cisalpinus Brongniart, Marinoni, 1877 (pp 16, 40 (pars)), Taramelli, 1881 (p 102 (pars)), Mariani, 1892 (p 40 (pars))

S cisalpina (Brongniart) Fuchs?, de Gregorio, 1894*b* (p 23)

S eichwaldi Fuchs, Frauscher, 1886 (p 41(77))

S granulosus Deshayes, Frauscher, 1886 (p 43(79))

S geniculatus d'Archiac, Frauscher, 1886 (p 42(78), Pl 5, fig 2)

S aegyptiacus Newton, 1898 (p 536, Pl 20, figs 4–6), Cossmann, 1901*b* (p 190 (20), Pl 2, fig 21), Oppenheim, 1903*a* (p 63, Pl 3, figs 1, 2), Newton, 1905 (p 169), von Klebelsberg, 1913 (pp 374, 375, 377), di Stefano, 1920 (p 24), Blanckenhorn, 1921 (pp 86, 88, 89, 90, 93, 94, 96), Weir, 1925 (pp 101, 107), Cuvillier, 1930 (pp 117, 122, 130, 163, 193, 196, 200, 208, 214, 222, 223, 225, 227, 263), Cuvillier, 1939 (p 1920), Rossi, 1942 (pp 159, 115, 125, 126, 129, 130, 121)

S aegyptuacus Newton, Pilgrim, 1908 (pp 21, 120)

MATERIAL *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2292, *2*, Reg No L 79940–1, FB F 2293, *1*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *2*), *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2313, *1*)

FURTHER DISTRIBUTION IN PAKISTAN Cox (1931*a*) has recorded the species from the Khirthar of the Bugti Hills, and from the Shekhan Limestone (Laki) of Kohat

FURTHER DISTRIBUTION This well-known species has been recorded from numerous localities, and the following is a summary of the distribution Libyan (Upper Ypresian) of Egypt, Lower Mokattam of Egypt, Lutetian of France (including Grignon, the type locality), Kressenberg, Mattsee, Italy, and north-east Bulgaria, Middle Eocene of northern Persia, Bahrein Island, Somaliland, the Balkans, Sirtica, and the Bavarian Alps, Upper Mokattam of Egypt, Auversian of France and Italy, Bartonian of Hungary and Switzerland, Upper Eocene of the Balkans and Sirtica, Eocene of the Aral Sea region, Russia, southern France, Spain, Switzerland, Somaliland and Croatia, Priabonian of Sirtica, Italy, France and southern Dagestan, Lower Tertiary of Russia and the Balkans (probably Eocene), and Nummulitic of southern France (probably Eocene)

REMARKS References to *Spondylus radula* Lamarck by Nyst, 1843 (Pl 25, fig 3), Nyst, 1845 (p 307), G Vincent, 1875 (p 31), G Vincent & Rutot, 1879 (p 120) and G Vincent & Rutot, in Mourlon, 1881 (p 179) have been shown by Glibert (1933) to be *S rarispina* Deshayes The form referred to *S radula* Lamarck by Frauscher, 1886 (pp 83, 249) has been renamed *S frauscheri* by Schlosser (1925*a*, 1925*b*) The forms from the Miocene of Spain referred to *S radula* Lamarck by Maureta & Thos y Codina, 1881 (p 372), Mallada, 1883 (p 57) and Mallada, 1892 (p 215) must refer to some other species, as *S radula* seems to be confined to the Eocene The species apparently ranges from Ypresian to Priabonian

SPONDYLUS ROUAULTI d'Archiac & Haime, 1854

REFERENCES *Spondylus rouaulti* d'Archiac, 1850*b* (*nomen nudum*) (3, 272), d'Archiac & Haime, 1854 (pp 272, 359, 368, Pl 24, figs. 6–8), Blanford, 1876 (p. 12), Mallada, 1878 (pp 323, 407), Medlicott & Blanford, 1879*b* (p 453), Duncan, 1880 (p 8), Blanford, 1880 (pp 40, 143), Fedden, 1880 (p. 204), Mallada, 1882 (Pl. 10, fig 6), Zittel, 1883 (pp 92, 99, 107, 110, 126), Cya, 1883 (p 55), Mallada, 1892 (p 200), Oppenheim, 1903*a* (p 65, Pl 3, figs 5, 5*a*), Douvillé, 1916 (pp 28, 45, Pl 9, figs 5, 6), Blanckenhorn, 1921 (pp 86, 90), A M Davies, 1923 (pars) (p 586), Cotter, 1926 (pp 412, 413, 415), Cuvillier, 1930 (pp 121, 163, 198, 200, 204, 206, 263), Cox, 1931*a* (pp 67, 34, 35), Cox, in Col Davies & Pinfold, 1937 (p 71), Rossi, 1942 (pp 160, 115, 129, Pl 8, fig 9)

S renaulti d'Archiac & Haime, Wynne, 1872 (p 253)

S roualti d'Archiac, Maureta & Thos y Codina, 1881 (p 321), Cotter, in Cossmann & Pissarro, 1927 (p 4)

S hispanicus Doncieux, 1911 (p 37, Pl 6, figs 12, 13)

S alexandrae Vredenburg, in Cossmann & Pissarro, 1927 (p 11, Pl 2, figs 11–13)

?*S roxanae* Vredenburg, in Cossmann & Pissarro, 1927 (p 12, Pl 2, figs 10, 14), Krishnan, 1943 (p 427)

Material *Zinda Pir section* Zinda Pir Limestones (lower part, local zone 1) (FB F 2712, *2*), *Kohat area* (*Shekhan Nala section*) Nummulite Shale (local subzone 4*b*) (FB F 2354, *1*), *Kohat area* (*Sirki Paila*) Sirki Shale/Kohat Limestone (local subzone 4*d*) (FB F 2114, *2*)

Accessory sample *Kohat area* (*Tarkhobi*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2191, *2*)

Further distribution in India and Pakistan Upper Ranikot (zone 3) in the hills south-east of Leilan old coal-pit on road to Unerpur (type locality for *S alexandrae*), Upper Ranikot (zone 4) in the hilly ground south-east of Petiani below big scarp of white limestone and north-west of Kotri (type locality for *S roxanae*), probably Laki of the Salt Range, Khirthar of Wagot The type locality is in the 'Hala Range'

Further distribution Ranikot (*Spondylus* Limestone Shales = Bed 14) 3 miles above Kampa Dzong (Tibet), Libyan of Egypt, Ypresian of southern France, Lower Mokattam of Egypt, Middle Eocene of Spain, Upper Mokattam of Egypt, Upper Eocene of Sirtica

SPONDYLUS SUBAEQUIVALVIS n sp

(Figures 46*a*, *b*, *c*, plate 11)

Material *Rakhi Nala section* White Marl Band (local zone 11) (FB F 1970, *7*, Reg No L 79871–3), *Zinda Pir section* White Marl Band (local zone 11) (FB F 2734, the holotype, Reg No L 79942, FB F 2546, *1*)

Description Shell moderately large, moderately thick-shelled, orbicular, strongly inflated, subequivalve, apparently equilateral, not gaping Umbos small, not prominent Dorsal margin obscured by matrix Outline almost circular Where the shell is broken, the internal mould shows that the internal surface of the shell was lirate Ornament consisting of spinose radial ribs of four orders, the difference in strength between those of any one order and the next not being very great The first order of ribs has one median intercalary rib, and between this second order rib and the primaries there are two ribs of the third order Ribs of the fourth order indicated by a single line of small spines projecting through the matrix on parts of the shell Spines all quite small, consisting of fairly closely spaced projections directed ventrally

Dimensions Holotype length 52 5 mm, height 46 5 mm, thickness (both valves) 40 3 mm

Remarks This species is closely related to *Spondylus asiaticus* d'Archiac, in Tchihatcheff (1866, p 150, Pl 4, figs 7,*a*,*b*), from the Eocene of Asia Minor, but is not so high, is still more inflated, and the intercalary ribs are more uniformly distributed, as are the small spines

Family Dimyidae

Genus *DIMYA* Rouault, 1850

(*Mem Soc Géol Fr* (2) 3, 470)

Type species *Dimya deshayesiana* Rouault, Eocene, monotypy

Synonyms *Deuteromya* Cossmann, 1903 (*Rev crit Paleozool* p 68) (replacement name)

Remarks *Deuteromya* was an unnecessary replacement name for *Dimya* Rouault, 1850 *non* Menke, 1828, Menke's name actually referring to a suborder (see Neave, 1939, 2) Thiele (1934) regarded the name *Marganona* Dall, 1882 as a synonym of *Dimya*, but in the original reference as given by Neave (1940, 3) only a brief reference to the genus is made by Kobeldt, no species being mentioned

DIMYA RAKHIENSIS n sp

(Figures 47, 48, 49*a*,*b*, plate 11)

Material *Rakhi Nala section* Upper Chocolate Clays (lower part, local zone 12) (FB F 1973, the holotype, Reg No L 79943, and 5 topotypes, Reg No L 79944–8, FB F 1974,*6*, FB F 1975,*10*+, FB F 1976,*6*, FB F 2097,*1*, FB F 1977,*4*, FB F 1978,*1*, FB F 1983,*3*, FB F 2751, *3*), *Zinda Pir section* White Marl Band (local zone 11) (FB F 2546, *2*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, *2*, FB F 2537,*1*, FB F 2535,*10*+, FB F 2529,*1*)

Description Shell of only moderate size, not very large, obliquely suboval, produced antero-ventrally, somewhat ostreiform, inequivalve, the right valve being a little more convex than the left valve, but neither valve very strongly inflated Umbos small, pointed, not prominent, situated posterior to the median line at about three-tenths of the length Shell moderately thick Attachment area not very distinct, shell normally attached to small *Discocyclinas*, the impression of the small pillars of which leave the umbonal region of the shell with a much finer, rather more vermicular pattern than the ornament on the majority of the surface Usual ornament consisting of closely spaced, rather frilled and ostreiform ribs, the intervals between which vary from linear in the immature portions of the shell to distinct, but still a little narrower than the ribs themselves, in the adult portion of the shell These ribs apparently increase in number both by intercalation and bifurcation, and often have the appearance of being double Topotypes show pairs of fine, wide-spaced lirae on the internal surface of the valves, these are not present on the narrow marginal flange, but continue dorsally some distance over the main body cavity of the shell Dorso-laterally these are replaced by short, closely spaced, lirae which give the internal dorsal surface an obsolete taxodont appearance

Dimensions Holotype length 15 8 mm, height 15 8 mm, thickness (both valves) 5 0 mm

Remarks *Dimya crearoi* Oppenheim (1900*a*, p 127, Pl 3, figs 15–19*a*), from the Eocene of Monte Postale, has stronger ornament and is a little smaller and less lamellar *Plicatula* *pamplonensis* Carez (1881, p 310, Pl 8, figs 2–5)—which also appears to be a *Dimya*—is smaller, narrower and less distinctly ornamented, Carez's species is from the Eocene of Spain *Anomia intusstriata* d'Archiac (1850*a*, p 441, Pl 13, figs 9–11), from the Nummulitic of Trabay near St Colombe, is slightly smaller, one valve appears to be more convex, and the ornament is finer and sharper, this species was figured by Fabiani (1908, p 181, Pl 4, fig 12) as *Dimya intusstriata*, but his form is higher, and the interior of the ventral region does not display distinct bipartite lirae

DIMYA(?) *SPONDYLIFORMIS* n sp

(Figures 51, 52*a*,*b*,*c*,*d*, 53, plate 12)

Material *Rakhi Nala section* Upper Chocolate Clays (lower part, local zone 12, upper part) (FB F 1984, the holotype, Reg No L 79949, and many topotypes, Reg No L 79950–9, FB F 1985, many specimens), *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2527, 2, FB F 2526, 2)

Description Shell small, suborbicular, tending to subquadrate when the dorsal margin is straighter than usual, fairly thick-shelled for its size, inequivalve, the right valve sometimes being a little more inflated than the left valve, sometimes markedly so Right valve attached, the attachment area usually occupying about a quarter of the height of the shell, rarely being very small, sometimes as large as half the area of the valve Right valve usually rather strongly inflated, but in some cases distinctly flatter, although still more inflated than the left valve Left valve more or less flat, sometimes vaguely swollen in the umbonal region and slightly concave elsewhere Outline suborbicular with a slight tendency to straightening of the dorsal margin, it is, however, variable, and there are many specimens which are subrectangular in outline, higher than wide, with a straight dorsal margin which is a little shorter than the width of the shell, and with somewhat flattened anterior and posterior margins The region of the prodissoconch seems to have been rather thin-shelled, as there is often a hole in the shell here, or an actual indentation of the dorsal margin, this feature, however, has no relation to the byssal foramen or plug of members of the Anomiidae Specimens with the straighter dorsal margin have the appearance of being subalate On the left valve of the holotype, where the shell is thinner, indications of two strong ridges meeting at an angle of about 90° can be seen through the shell in the umbonal region, these are apparently the margins of the resilifer Ornament beautifully preserved and very constant in character, consisting of a regular lattice-work of radial ribs and concentric threads of about the same strength, producing rounded crenulations at their points of intersection, there is a tendency for the radial ribs to predominate in the umbonal region (below the attachment area) on the right valve Although numerous specimens are available, they are either fragmentary ventral and median portions of valves, or specimens with both valves in contact, consequently the hinge characters have not been seen A portion of a left valve shows interiorly a slightly concave portion about half the height of the shell and in which the main part of the body of the animal evidently lived, that portion of the shell ventral to this concave area is flattened, a narrow ventral portion being even somewhat out-turned On the main flattened portion there is a series of slightly wavy lirae, arranged usually in pairs, occasionally in threes The groups are moderately wide-spaced, and there are occasional intercalary groups which are sometimes closer to the next posterior group and do not extend so far dorsally Lirae not present on the concave portion of the valve or on the out-turned ventral flange, and appearing to be a little stronger at their ventral extremity There are 14 groups on the specimen illustrated Dorso-laterally, these are replaced by rather close-spaced, short lirae, not in pairs, on the narrow flange-like area bordering the cavity of the umbonal region

Dimensions Holotype length 5 4 mm , height 5 6 mm , thickness (both valves) 2 25 mm Topotype length 5 8 mm , height 6 0 mm , thickness (both valves) 2 6 mm

Remarks Superficially this form resembles some members of the Anomiidae, but it had a definite area of attachment, lacked any true byssal foramen or plug, was not, apparently, subnacreous, and the valves were internally lirate, the left valve, at any rate, also appears to have had two strong ridges bounding the resilifer, rather than crura The subalate dorso-lateral margins, the often straight dorsal margin and non-projecting umbos, and the fact that the valve margins are internally lirate rather than fluted, induce the writer to believe that the species is better placed provisionally under *Dimya* than under *Spondylus* or *Plicatula* There does not appear to be any closely related species

Superfamily Ostracea

Family Ostreidae

Genus *OSTREA* Linné, 1758

(*Syst Nat* 10th ed p 696)

Type species *Ostrea edulis* Linné, Recent, Children, 1823

Synonyms *Peloris* Poli, 1791 (not binomial) (*Test Sicil* 1, Introd p 33)

Peloriderma Poli, 1795 (not binomial) (*Test Sicil* 2, 255, 261)

Eostrea Jhering, 1907 (*An Mus Nac B Aires*, (3), 7, 42) If the type species has not been designated it should be chosen from the two Recent species *Ostrea puelchana* d'Orbigny and *O spraeta* d'Orbigny

Anodontostrea Suter, 1917 (*N Z Geol Soc Pal Bull* no 5, p 86), Type species *Ostrea angasi* Sowerby, Recent, Finlay, 1928

Monoeciostraea Orton, 1928 (*Nature*, 121, 321) (a replacement name for *Ostrea*)

Bellostrea Vialov, 1936 (*C R Acad Sci U R S S* 4, 17), type species *Ostrea bellovacina* Lamarck, Eocene, monotypy

Remarks *Eostrea* was founded on the basis of crenulations on the interior of the valve margins There appear to be many intermediate forms between these and the typical *Ostrea* with smooth valve margins, and consequently *Eostrea* is not regarded as being of any systematic importance

OSTREA MULTICOSTATA Deshayes, 1832

References *Ostrea multicostata* Deshayes, 1832*a* (p 363, Pl 57, figs 3–6), d'Archiac, 1850*b* (pp 37, 38 (pars), 274 (pars)), Bronn, 1853–6 (p 352, Pl 36^2, figs 6,*a*,*c*), Coquand, 1862 (pars) (pp 111, 115, 116, 118, 125, 127, 132), Fischer, 1871 (p 230), E Pavay, 1871 (pp 370, 425), Wynne, 1872 (p 253, referred to d'Archiac), Ball, 1874 (p. 155), Blanford, 1876 (p 21), Blanford, 1880 (p 68), Zittel, 1883 (pp 103, 105, 111), Romanowski, 1884 (p 39, Pl 3 bis, figs *5a,b*), Frauscher, 1886 (pars) (pp 62, 39), Cossmann, 1887 (p 194), Boghdanovich, 1890 (p 66), Harris & Burrows, 1891 (p 77), Koch, 1894 (pp 228, 240, 243), Thomas, 1899 (pp 47, 48), Noetling, 1901 (pp 55, 107, 110), Oppenheim, 1903*a* (p 29, Pl 1, figs 1, 8–11), Cossmann & Pissarro, 1904*a* (Pl 44, fig 135–28), Chautard, 1905 (pp 148, 144, 145, 146, Pl 5, fig 2), Vredenburg, 1908*a* (p 315), Vredenburg, 1908*b* (pp 315, 316, 317), Holland, 1908 (p 20), Roussel, 1909 (pars) (pp 875, 876), Dareste de la Chavanne, 1910*a* (p 41), Dareste de la Chavanne, 1910*b* (pp 114, 115, 127, 142, 150), Douvillé, 1911 (p 641, Pl 10, figs 2, 3), Hayden, 1911 (p 63), Middlemiss, 1914 (p 110 (pars)), Gorizdro, 1915 (pp 28, 29, 50), Fischer & Wenz, 1918 (p 63), di Stefano, 1920 (pp 33, 36), Douvillé, 1920*b* (p 158), Douville, 1920*a* (pp 160, etc , Pl 4, fig 2), Blanckenhorn, 1921 (pp 75–76, 78, 88, 84), Astre, 1922 (pp 141, etc), Trechmann, 1923 (p 362, Pl 16, figs 1, 1*a*), Jackson, 1926 (p 352), Cossmann & Pissarro, 1927 (p 8), Moret, 1928 (p 1152), Cuvillier, 1930 (pp 57, 59, 60, etc), Yang Kieh, 1930 (pars) (pp 89, 78, etc , Pl 6, figs 1–4, 8, 9, 10, 11, Pl 7, fig 1), Cox, 1931*a* (pp 62, 27, 34, Pl 3, fig 1), Pérébaskine, 1932 (p 62), Bédé, 1933 (p 282 (pars)), Vialov, 1934*b* (p 46), Bornemann, Buraček & Vialov, 1934 (pp 256, 257, 258), Vialov, 1934*c* (p 535), Laffitte, 1934 (pp 1637, 1638), Vialov, 1935 (p 280), Pieragnoli, 1935 (p 162), Vialov, 1936 (pp 23, 32), Jacquet, 1936*a* (p 336), Jacquet, 1936*b* (pp 1273, 1274), Leriche, 1936 (pp 1249, 1253), Coulon, 1936 (p 33), Cuvillier, 1937 (pp 63, 65), Vialov, 1937 (pp 1628, 1637), Cox, 1938*a* (pp 34, 35), Vialov, 1938 (p 17), Cuvillier, 1938 (p 152), Stefanini, 1938 (p 14), Flandrin, 1938 (p 121), Moret, 1938 (pp 35, 46), Furon, 1941 (p 335), Furon & Soyer, 1947 (p 59, Pl 5, fig 135–28)

O multicostata? Deshayes, Wood, 1861 (p 28, Pl 6, figs 3*a,b*), Newton, 1891 (p 4)

O flabellula Lamarck, Medlicott & Blanford, 1879*b* (p 463 (pars)), R D Oldham, 1893 (p 310 (pars))

O strictiplicata Locard, 1889 (p 57 (pars)), Pl 10, figs 7*a,b*, Pl 11, figs 2, 3, *non* figs 1, 1*a*, 4, 4*a*)

O elegans Deshayes var *cornigera* Mayer-Eymar, Oppenheim, 1903*a* (p 20, Pl 17, figs 2, 6)

O multicostata Deshayes var *cornigera* Mayer-Eymar, Desio, 1934 (pp 110, 86, Pl 8, figs 6*a,b*)

O multicostata Deshayes var *intermedia* Cuvillier, 1935 (p 2, Pl 1, figs 5, 6)

MATERIAL *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1895,*1*), Rubbly Limestones (local zone 6) (FB F 1906,*1*, Reg No L 79960), Shales with Alabaster (local zone 7) (FB F 1920,*1*, FB F 1921,*2*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294,*1*), *Kohat area* (*Shekhan Nala section*) Nummulite Shale (local subzone 4*b*) (FB F 2354, *1*), Kohat Limestone (local subzone 4*b*) (FB F 2356,*1*)

FURTHER DISTRIBUTION IN INDIA AND PAKISTAN The species has been recorded by Cox (1931*a*) from the Lower Ghazij Shales of Harnai, from the Laki of Hyderabad District, Sind, and Palana, Bikanir State, Rajputana, from the Khirthar of Wagot, Cutch (by Wynne (1872) also), and the 'Alore' Hills, Sind, and from beds probably of Khirthar age in the Giri Valley, Subathu

Further distribution This well-known species has a wide distribution which may be summarized as follows London Clay of England, Cuisian of the Paris Basin, Suzak Beds (Lower Eocene) of Boukhara, Lower Libyan of Upper Egypt, Lower Eocene of Algeria, the Arabian Desert, central Asia, and the French Sudan, Middle or Lower Eocene of Guelma, Lower Mokattam of Egypt, Alai Stage (Middle Eocene) of Ferghana, Russia, Bracklesham Beds of Bracklesham Bay, Middle Eocene of the Arabian Desert, the Sudan, Senegal, Belgium, Somaliland, Jamaica, Turkistan and Hungary, Upper or Middle Eocene of Somaliland, Upper Mokattam of Egypt, Eocene of Constantine, the Suez isthmus, the northern Alps, central Asia, the Balkans, Algeria, Egypt, Morocco, north of Khanabad, the Sudan, France and Afghanistan, and derived in post-Eocene beds in Upper Egypt

Remarks The distinction of this species from *Ostrea strictiplicata* Locard is based on the work of Astre (1922) Those Eocene forms from India and Pakistan that were referred to as *O flabellula* Lamarck by Medlicott & Blanford (1879*b*) and R D Oldham (1893) belong to this species The varieties *cornigera* Mayer-Eymar and *intermedia* Cuvillier seem to be mere variants rather than distinct varieties Mallada's 1883 illustrations (Pl 11, figs 7, 8) of *O multicostata* (incorrectly referred to d'Archiac) are copied from d'Archiac & Haime (1854) and are thus *O subangulata* (d'Orbigny)

OSTREA PSEUDOPUNICA n sp

(Figures 54*a*, *b*, 55, 56, 57, plate 12)

Material Lower Chocolate Clays east of Safaed, south of Tobah, Dera Ghazi Khan District—the holotype, Reg No L 77893, and 4 topotypes, Reg No L 77889–92—from Mr Pinfold's collection *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1929, *1*), Lower Chocolate Clays (local zone 11/10) (FB F 1962, the paratype, Reg No L 79961, and 4 other specimens, Reg No L 79962–5)

Description Shell of moderate size, irregularly suboval, distinctly thick-shelled, especially in the umbonal region of the left valve

Left valve gently to moderately inflated, with an attachment area of variable size—in one case the left valve is attached to another long narrow *Ostrea* so that the attachment area extends from umbo to ventral margin Outline of holotype fairly regularly oval, but in other specimens less regular Umbo always strongly opisthogyrous, as is the internal resilifer Ornament constant and characteristic, the scaly and rather lamellar growth lines being crossed by numerous fine rather closely spaced ribs Intervals between the ribs rather narrow, the ribs tending to be interrupted and frilled by the growth lamellae Resilifer internally very strongly curved over backwards, sometimes actually ending on the dorsal exterior shell surface Excavated portion of shell in which the main portion of the body of the animal evidently lodged bordered ventrally by an irregularly flattened, flange-like area which is one-third the height of the valve in the holotype Ventral margin of hinge line fairly straight Flattened ventral flange continuing laterally as a relatively narrow band right to the ends of the ventral margin of the hinge line, it is narrow and excavated on the dorsal half of the shell, where it is ornamented with an irregular series of transverse crenulations or ridges, equal to or narrower than the width of their intervals, the posterior row being almost divided into two longitudinal portions by the concavity of the narrow flange This zone of irregular crenulations extends round the ventral portion of the shell, close to the outer margin of the flange Ventrally, where the flange is widest, there are sometimes indications of faint radial incised lines extending from the crenulated zone to the dorsal margin of the flange In another, somewhat smaller, specimen, the crenulations are obsolete ventrally and laterally, and dorso-laterally they have fused to some extent, on a still smaller specimen, the fusion is still more marked, and the appearance is that of a band with a number of rounded pits which become more elongate on the ventral portion of the shell Muscle scar situated slightly below and a little behind the middle of the shell, broadly quarter-moon shaped, with the points directed upward

Right valve a little narrower in its dorsal outline, its posterior and ventral margins meeting in a rounded angle of about 90° instead of being more regularly curved Umbo strongly opisthogyrous, as is the internal resilifer Surface flat and smooth except for regular growth lamellae Dorso-lateral margins flattened in a plane at right angles to the plane of commissure, the flattened area carrying a distinct, irregularly continuous series of fine radial riblets which are of the same width as or slightly narrower than their intervals Ventral margin of hinge line projecting inwards into the shell cavity, the resilifer itself sloping dorsally and upwards away from the plane of commissure of the valves Lateral and ventral margins carrying a band of irregular, distinct crenulations along their edge which tends to be slightly raised, and is not comparable, in its lateral portions at any rate, with the narrow depressed zone of the left valve Valve margins, a little below the hinge line, tending to project inwards towards the plane of commissure of the valves Crenulations less prominent round the ventral margin, more than one row sometimes being seen when the surface is worn Muscle scar similar in position to that of the left valve, but the dorsally directed points more distinct

Dimensions Holotype (a left valve) length 37 1 mm , height 42 2 mm , thickness (one valve) 12 9 mm Paratype (a right valve) length 35 1 mm , height 38 3 mm , thickness (one valve) 7 3 mm

Remarks The ribbing on the left valve is finer and more uniform, and does not become obsolete ventrally on adult shells compared with *Ostrea punica* Thomas (1893, p 12, Pl 13, figs 1–5), from the Upper and Lower Suessonian of Tunisia The umbos are also less pointed and more enrolled

OSTREA RAKHIENSIS n sp

(Figure 50, plate 11)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1900, the holotype, Reg No L 79966)

Description Left valve (the only specimen available) of moderate size, very high, and of elongate-oval outline, somewhat irregular, the anterior margin being gently convex, the posterior margin slightly sinuous (concave dorsally), and the ventral margin only slightly convex Median and posterior surface of the valve flattened, ornamented with numerous, fine, delicate, concentric folds, and separated from the moderately narrow anterior ribbed portion of the shell by a distinct carination Ribs of moderate size and strength, slightly wider than their intervals Umbo very strongly enrolled and opisthogyrous, as is the resilifer on the interior Ribbed portion of shell forming an angle of 90 to 110° with the relatively smooth, flattened portion

Dimensions Holotype length 24 0 mm , height 47 6 mm , thickness (left valve only) 13 3 mm

Remarks The form and ribbing, as also the nature of the large flattened area, are apparently characteristic The latter is not an area of attachment The shell in life seems to have lain unattached on a muddy sea floor

Subgenus *LIOSTREA* H Douvillé, in J de Morgan, 1904

(*Mission scientifique en Perse*, 3, pt 4, p 273)

Type species *Ostrea sublamellosa* Dunker, Rhaetic, monotypy

Synonyms *Flemingostrea* Vredenburg, 1916 (*Rec Geol Surv Ind* 47, 196) Type species *Ostrea flemingi* d'Archiac & Haime, Eocene, by tautonymy

Sinustrea Vialov, 1936 (*C R Acad Sci U R S S* 4, 18) Type species *Ostrea morgani* Vredenburg, Upper Cretaceous, monotypy

Remarks The retention of *Flemingostrea* Vredenburg (as a subgenus of *Ostrea*) and the erection of *Sinustrea* as a section of *Liostrea* by Vialov seem to be unjustified Specimens from western Pakistan and western India show that the presence or absence of fine radial ornament or of a ventral sinuosity of the valve margin does not even have any specific value

OSTREA (*LIOSTREA*) *PSEUDOFLEMINGI* n sp

(Figures 58, 59, 60*a*, *b*, 61, 62*a* to *d*, plate 12)

References The only really satisfactory records of *Ostrea* (*Liostrea*) *flemingi* d'Archiac & Haime are from the Laki (see Cox, 1931*a*) The examination of numerous collections from the Eocene of western Pakistan and western India has convinced the writer that, in spite of the difference in form displayed by the two species, all the Khirthar records of *O* (*Liostrea*) *flemingi* for at least 85 years really refer to *O* (*L*) *pseudoflemingi* The specimens concerned in these old records are not readily available, and it is expected that their reference to *O* (*L*) *pseudoflemingi* will at some time be confirmed, the references concerned are

O flemingi d'Archiac, Medlicott, 1864 (p 100), Wynne, 1868 (p 30), Blanford, 1869 (pp 64, 208), Ball, 1874 (p 155)

O flemingi d'Archiac & Haime, Wynne, 1872 (pp 238, 256), Medlicott & Blanford, 1879*a* (p 340 (pars)), Medlicott & Blanford, 1879*b* (p 506 (pars)), Blanford, 1880 (p 68), R D Oldham, 1893 (p 301 (pars)), Krishnan, 1943 (p 449)

O (*Liostrea*) *flemingi* d'Archiac & Haime, Cox, 1931*a* (pp 63, 34 (pars))

Material *Rakhi Nala section* Green and Nodular Shales (local zone 5) (FB F 1887,*4*), Rubbly Limestones (local zone 6) (FB F 1908,*1*, FB F 1910,*2*, FB F 1912,*2*, FB F 1913, *9*, FB F 2055,*10*+, FB F 1916,*6*, FB F 1919,*6*), Shales with Alabaster (local zone 7) (FB F 1922,*6*, FB F 1924,*6*), Lower Chocolate Clays (local zone 11/10) (FB F 1962, the holotype, Reg No L 79967, and a large number of topotypes, Reg No L 80617–25), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2559,*50*+, FB F 2558,*1*, FB F 2557,*10*+, FB F 2556,*10*+, one Reg No L 79912, FB F 1555,*10*+, FB F 2567,*6*, FB F 2569, *6*, FB F 2566, *1*, FB F 2732, *10*+, FB F 2565, *10*+, FB F 2554, *10*+, FB F 2568, *10*+, including one figured syntype, Reg No L 79968–73, FB F 2563, *10*+, FB F 2553, *10*+, FB F 2731, *6*, FB F 2552, *6*, FB F 2551, *10*+), White Marl Band (local zone 11) (FB F 2734, *10*+), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230/2294, *1*), Kaladhand Limestone (local subzone 4*a*) (FB F 2255, *1*), *Kohat area* (*Shekhan Nala section*) Nummulite Shale (local subzone 4*b*) (FB F 2352, *1*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *1*)

Description Shell of moderate size, subequivalve, the right valve a little more convex than the left valve, inflation moderate, left valve sometimes rather flattened, especially umbonally Outline irregularly suboval-subquadrate, a little oblique, somewhat drawn out postero-ventrally, the dorsal margin tending to be straight on account of the alate dorso-lateral margins The ventral margin has a sinuosity (sinus on left valve, and fold on right valve) which varies from almost nil to quite marked Ornament consisting of growth lines and concentric growth lamellae, under certain conditions of preservation obscure, moderately fine radial riblets can be seen in the umbonal regions of both valves Internally, the resilifer is wide, the valve margins smooth, and the adductor muscle impression subcircular in outline (but with a flattened dorsal margin) and usually situated distinctly below and behind the middle The resilifer is fairly wide, and is not curved

Dimensions Holotype length 28 7 mm, height 33 0 mm, thickness (both valves) 16 0 mm A topotype length 28 4 mm, height 33 2 mm Another topotype length 19 1 mm, height 23 9 mm A syntype length 39 4 mm, height 41 4 mm, thickness (both valves) 19 0 mm

Further distribution in India and Western Pakistan The distribution of the forms given in the references above, and which may in all likelihood belong to this species, is as follows Khirthar of Bhodan (near Surat, in the Tapti River Valley), probably Khirthar of Lukput (Cutch), Eocene (?Khirthar) of Subathu, gypseous shales (Khirthar) of Wag-ka-pudder (Cutch) Ball (1874) recorded a form, which is probably this species, from stage (*e*) of the Eocene in the Luni Pathan Hills, south-east Afghanistan, this is probably the record subsequently referred to as 'Suleiman Hills' (in Western Pakistan) by later authors

Remarks This species has a much wider dorsal margin and resilifer, and is much more alate and with less prominent umbos than *Ostrea* (*Liostrea*) *flemingi* d'Archiac & Haime with which it has apparently been confused *O* (*Liostrea*) *morgani* Vredenburg (1916, p 197, Pls 17, 18), from the Maestrichtian of the Des Valley, is not bialate, having much more pointed and prominent umbos *O* (*Liostrea*) *kalhora* Vredenburg (1916, p 199, Pl 19, Pl 20, fig 8), from zone 3 of the Upper Ranikot at Jherruck, and from zone 4 of the Upper Ranikot at Jherruck and north-east of Kotri, although somewhat bialate, is not so markedly bialate as *O* (*Liostrea*) *pseudoflemingi*, and, moreover, has much more distinct radial ornament *O chudeaui* Douvillé 1920 (1920*a*, p 163, Pl 4, figs 9, 10, 11), from the Eocene of the Sudan, is superficially very similar, especially in outline, but the lower valve has three distinct ribs and is evidently an *Ostrea, sensu stricto* *Vulsella aymari* Oppenheim as figured by Desio (1934, p 95, Pl 7, fig 6, Pl 11, figs 9*a*, *b*), from the Eocene of Egypt, bears a superficial resemblance to *Ostrea* (*Liostrea*) *pseudoflemingi* but is smaller and higher Cossmann (1922*a*, pp 211–212, Pl 11, figs 30–37) used a new subgeneric name *Biauris* for *Ostrea* *subhippopodium* d'Archiac, from the Bartonian of southern France (the reference is not p 70 as given by Neave, 1939) While of somewhat similar aspect, this French form is not so high, and the adductor muscle impression is distinctly above the median line

OSTREA (*LIOSTREA*) sp A

References *Ostrea* (*Liostrea*) cf *rouaulti* Mallada, Cox, 1931*a* (pp 63, 27, 28, 34, Pl 3, figs 5–8), Cox, in L M Davies & Pinfold, 1937 (p 11), Vokes, 1937 (p 4)

O (*Liostrea*) *roualti* Mallada, Cotter, 1933 (p 98)

Material *Kohat area* (*Panoba section*) Lower Chharat (*Ostrea* Alternations, local zone?) (FB F 2242, *1*), Lower Kohat Shales (local subzone 4*a*) (FB F 2251, *1*, FB F 2252, *11*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *15*+, FB F 2255, *1*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *1*), *Kohat area* (*Shekhan Nala*) Kaladhand Limestone (local subzone 4*a*) (FB F 2334, *1*, FB F 2376, *1*, FB F 2336, *2*), Upper Kohat Shales (local subzone 4*a*) (FB F 2341, *1*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *1*)

Further distribution in Western Pakistan and India Ghazij Shales of Hindu Bagh, Sakesar Limestone of the Salt Range, Lower Subathu (Khirthar) 5 miles north-west of Arki (21 miles north-west of Simla), Kohat Shales of Bahadur Khel, and Kohat

Subgenus *LOPHA* Bolten, in Roding, 1798

(*Mus Bolt* pt 2, p 168)

Type species *Ostrea cristagalli* Gmelin, Recent, Dall, 1898

Synonyms *Alectryonia* Fischer von Waldheim, 1807 (*Mus Demid* 3, 269), the type species, if not already selected, should be chosen from the following four species in the original list *Alectryonia rara* F von Waldheim = *Mytilus crista-galli* Linné, *Alectryonica parasitica* F von Waldheim, Recent, *A hyotis* F von Waldheim, Recent = *Ostrea hyotis* Chemnitz, and *Alectryonia frons* F von Waldheim, Recent = *Ostrea frons* Chemnitz

Dendrostraea Swainson, 1840 (*Treat Malacol* p 380), type species *D folium* (Sowerby), Recent, Gray, 1847

Dendrostrea Agassiz, 1846 (*Nomencl Zool Index Univ*) (amended spelling)

Dendostrea auct (amended spelling)

Nicaisolopha Vialov, 1936 (*C R Acad Sci U R S S* 4, 20), type species, *Lopha* (*Nicaisolopha*) *nicaisi* Coquand, Cretaceous, monotypy

Cameleolopha Vialov, 1936 (*C R Acad Sci U R S S* 4, 20), type species, *Lopha* (*Cameleolopha*) *cameleo* Coquand, Cretaceous, monotypy

Abruptolopha Vialov, 1936 (*C R Acad Sci U R S S* 4, 20), type species, *Lopha* (*Abruptolopha*) *abrupta* d'Orbigny, Cretaceous, monotypy

Remarks The subgenus *Nicaisolopha* was defined as having vague folds, *Cameleolopha* was defined as being characterized by a few dichotomous ribs, and *Abruptolopha* was defined as possessing very numerous dichotomous ribs Variation in degree of strength, and even in type of ornament within the Ostreidae, within such limits, does not appear to be of any systematic importance, and these forms are therefore treated as synonyms of *Lopha*

OSTREA (*LOPHA*) *MELANIA* d'Orbigny, 1850

(Figures 63*a*,*b*,*c*, plate 12)

REFERENCES *Ostrea orbicularis* J de C Sowerby, 1839 (p 328, Pl 24, fig 8) *non* Linne, 1758, Sykes, 1839 (p 718), d'Archaic, 1850*b* (p 275), d'Archaic & Haime, 1854 (pp 169, 368), Carter, 1854 (p 252), Cox 1931*a* (p 66), Krishnan, 1943 (p 451)

O melania d'Orbigny, 1850 (p 327)

O martinsii d'Archaic, Cox, 1931*a* (p 66 (pars))

O (*Alectryonia*) *martinsi* d'Archiac, Frauscher, 1886 (pars) (pp 68–69, *non* Pl 3, figs 4–6)

Alectryonia martinsi (d'Archiac), Weir, 1925 (pp 101, 107 (pars))

Alectryonia cf *martinsi* (d'Archiac), Newton, 1905 (p 166, Pl 20, figs 1, 2)

MATERIAL *Rakhi Nala section* Upper Chocolate Clays (lower part, local zone 12) (FB F 1979, *4*, FB F 1983, *1*, Reg No L 79974), *Pellatispira* Beds (local zone 15) (FB F 1981, *1*)

FURTHER DISTRIBUTION IN INDIA Khirthar of Luckput, Cutch (type locality), and of the hills 12 to 15 miles north of Booj, Cutch

FURTHER DISTRIBUTION Eocene of Dobar (south of Berbera, Somaliland)

REMARKS d'Orbigny in 1850 renamed J de C Sowerby's *Ostrea orbicularis*, a name pre-employed by Linné in 1758, *O melania* d'Orbigny's name has often been overlooked, and also several times placed in the synonymy of *O martinsii* d'Archiac Several other forms from Italy, the northern Alps and France have also been referred to *O martinsii*, some of them obviously incorrectly Compared with the original illustration of *O martinsii* d'Archiac, *O* (*Lopha*) *melania* is not so large and the ribs are less radial in disposition from a point well below the umbos, the ribs are more regular and apparently less scaly Schlosser (1925, p 37) was correct in pointing out that Frauscher's figures (1886, Pl 3, figs 4, ?5, 6) of *O martinsi* from the Eocene of the northern Alps differed from d'Archiac's original illustration, he referred them to *Alectryonia alticostata* Mayer, a species which apparently differs from *Ostrea* (*Lopha*) *melania* in being of somewhat smaller size and in having heavier, broader and more rounded ribs Frauscher's fig 5, incidentally, seems to belong to still another species as the ribbing is almost completely obsolete Oppenheim's (1900*a*) illustrations (Pl 7, fig 2, Pl 12, figs 14, 14*a*) of *O* (*Alectryonia*) *martinsi* d'Archiac from the Priabonian of northern Italy seem to show still another form which is larger, more explanate and with more numerous and dichotomizing ribs posteriorly than *O* (*Lopha*) *melania* Cossmann's (1922*a*, Pl 12, figs 18–21) illustrations of *Alectryonia martinsi* (d'Archiac) from the Lutetian of Bastennes, especially his Figs 19 and 20, seem most closely comparable to Oppenheim's form Newton's illustrations (1905, Pl 20, figs 1, 2) of *A* cf *martinsi* (d'Archiac) from the Eocene of Somaliland agree with *Ostrea* (*Lopha*) *melania* in their smaller size, sharp V-shaped ribs and outline J de C Sowerby's original illustration of his *O orbicularis* is misleading in that the adherent matrix gives it an orbicular outline, whereas the species actually has the form of the specimen here figured In view of the differences mentioned above between the various forms, it seems advisable to retain d'Orbigny's name for Sowerby's species from Cutch, a species which appeared to exist in Somaliland, but which was represented by related forms in Egypt, Italy, France and the northern Alps

Subgenus *PYCNODONTE* Fischer von Waldheim, 1835

(*Bull Soc Nat Moscou*, **8**, 118)

Type species *Pycnodonte radiata* Fischer von Waldheim, Cretaceous = *Ostrea vesicularis* Lamarck, Gardner, 1916

Synonym *Pycnodonta* Swainson, 1842 (amended spelling) (*Conch Man* 2nd ed , p 85), type species *Pycnodonta radiata* (Fischer von Waldheim), Cretaceous, monotypy

OSTREA (*PYCNODONTE*) *BRONGNIARTI* (Bronn), 1831

References *Gryphea columba* (Lamarck), Brongniart, 1823 (p 10)

Gryphaea brongniarti Bronn, 1831 (p 122), E Pavay, 1871 (p 425), von Hantken, 1872 (p 85), Tournouer, 1872*b* (p 710), Frauscher, 1886 (pp 47, 48, 250, 252, 253, 258, 261, 262, *non* Pl 1, figs 11–14, Pl 2, figs 1*a*, 6 = *Ostrea* (*Pycnodonte*) *frauscheri* (Traub) 1938), Koch, 1894 (pp 225, 228), von Bukowski, 1898 (pp 584, 585), Athanasiu, 1899 (pp 266, 257), Oppenheim, 1900*a* (pp 18, 20), Oppenheim, 1901*a* (p 323), Oppenheim, 1903*b* (p 116), Dreger, 1903 (pp 255, 281), Popescu-Voitesti, 1910 (pp 137, 155), Weithofer, 1918 (p 90), Schlosser, 1922 (pp 259, 287, pars), Schlosser, 1925*a* (pp 35, 167), Vredenburg, 1928*b* (p 430), Reina, 1934 (p 2), Tomor-Thirring, 1935 (p 10), Vialov, 1937 (p 1635), J Noszky, 1939 (p 32)

G brongniarti d'Archiac, Fabiani, 1915 (pp 8, 66, 127, 155, 262, 266, 281)

Ostrea brongniarti (Bronn), von Hantken, 1872 (pp 81, 107), Tournouer, 1872*b* (p 718), Tournouer, 1872*a* (p 502), de Bouillé, 1873 (pp 430, 433, 436, Pl 7, fig 1), Tournouer, in de Bouillé, 1876 (pp 30, 39), Mallada, 1892 (p 199), Oppenheim, 1900*a* (p 7), Oppenheim, 1900*b* (p 238), Oppenheim, 1900*c* (pp 289, 341), Fabiani, 1908 (pp 65, 66), Newton, 1911 (p 637), Boussac, 1911*b* (pp 5, 82, 87), Cox, 1931*c* (p 235), Cox, in B Thomas, 1932 (p 364), Petruševskij, 1937 (p 82)

O brongniarti Bellardi, Carez, 1881 (p 223)

O (*Gryphaea*) *brongniarti* (Bronn), C Mayer-Eymar, 1887 (p 123), C Mayer-Eymar, 1893 (p 20), Koch, 1894 (p 223), Oppenheim, 1900*a* (p 120, Pl 7, fig 1), Oppenheim, 1900*c* (p 261, pars), Fabiani, 1908 (p 180), Dainelli, 1915 (pp 423, 77, 114), Fabiani, 1915 (pp 44, 55, 162)

O (*Gryphaea*) *beongniarti* (Bronn), K Mayer-Eymar, 1890 (p 170)

Exogyra brongniarti (Bronn), Oppenheim, 1896*b* (p 30)

Pycnodonta brongniarti (Bronn), Sacco, 1897*a* (pp 21, 22, Pl 7, figs 1, 2), Boussac, 1911*a* (pp 181, 408, Pl 9, figs 9,*a–c*, 10,*a–c*, 13,*a*, 17,*a–c*, Pl 10, figs 1, 2,*a*, 9, 21,*a*, 22,*a*), Dalloni, 1917 (pp 98, 103, 105, 110), Bornemann, Buraček & Vialov, 1934 (p 259), Korobkov, 1935 (pp 126, 127, 128), Flandrin, 1938 (pp 127, 145, Pl 14, fig 11, Pl 15, figs 31–33), Belmustakov, 1949 (pp 39, 53)

Ostrea (*Pycnodonta*) *brongniarti* (Bronn), Rovereto, 1897 (p 318(9)), Rovereto, 1900 (p 43, Pl 1, fig 1), Cox, 1931*a* (pp. 64, 29, 32, 34), Cotter, 1933 (p 97), Stchepinsky, 1941 (p 19, Pl 1, fig xix)

Pycnodonta brongniarti (Bronn) var *expansior* Sacco, 1897*a* (p 22, Pl 7, fig 3)

P brongniarti (Bronn) var *oblongula* Sacco, 1897*a* (p 22, Pl 7, fig 4)

P brongniarti (Bronn) var *parvulina* Sacco, 1897*a* (p 22, Pl 7, fig 5)

Ostrea (*Pycnodonta*) *brongniarti* (Bronn) var *planulata* Rovereto, 1897 (p 318(9)), Rovereto, 1900 (p 44)

O (*Pycnodonta*) *brongniarti* (Bronn) var *rostrata* Rovereto, 1900 (p 44, Pl 1, fig 1*a*)

O (*Pycnodonta*) *brongniarti* (Bronn) var *bisimpressa* Rovereto, 1900 (p 44, Pl 1, fig 1*b*)

Griphaea brongniarti (Bronn), Fabiani, 1915 (p 269)

Liostrea (*Pycnodonta*) *brongniarti* (Bronn), Cossmann, 1922*a* (p 213, Pl 12, figs 28–30)

Pycnodonta (*Gryphaea*) *brongniarti* (Bronn), Schlosser, 1925*b* (p 51)

Gryphea brongniarti (Bronn), Tomor-Thirring, 1935 (pp 9, 10, 11, 12)

Gryphaea (*Pycnodonta*) *brongniarti* Bronn, Venzo, 1938 (p 192), Venzo, 1939 (p 166)

G brongniarti Bronn var *exalata* J Noszky, 1939 (pp 32, 105)

Picnodonta brongniarti (Bronn) var *libyca* Rossi, 1942 (pp 155, 115, 139, 141)

Pycnodonta brongniarti (Bronn) var *libyca* Rossi, 1942 (p 138, Pl 8, figs 2*a*,*b*, Pl 9, figs 1*a*,*b*)

Ostrea callifera? Lamarck, J de C Sowerby, 1839 (p 328, Pl 24, fig 7), Carter, 1854 (p 252), Ball, 1874 (p 155)

O callifera Lamarck, Vickary, 1846 (p 267), d'Archiac, 1850*b* (pp 200, 273 (pars)), d'Archiac & Haime, 1854 (pp 167, 171, 368)

Gryphaea globosa? J de C Sowerby, J de C Sowerby, 1839 (p 328, Pl 25, fig 16)

G globosa J de C Sowerby, Carter, 1854 (p 296), Oppenheim, 1901*b* (p 231)

Ostrea globosa (J de C Sowerby), Blanford, 1880 (p 48)

O vesicularis Lamarck, d'Archiac, 1846 (p 213 (pars)), d'Archiac, 1850*a* (p 440), d'Archiac, 1850*b* (3, 197, 198, 275 (pars)), d'Archiac & Haime, 1854 (pp 274, 168, 358, 359, 368), Raulin & Delbos, 1855 (p 1153), Carter, 1857 (p 629), Blanford, 1876 (p 13), Duncan, 1880 (p 9 (pars)), Blanford, 1880 (pp 104, 127), L M Davies, 1925 (pp 210, 217), Krishnan, 1943 (p 429)

O vesicularis Lamarck var d'Archiac, 1850*a* (pp 440 (pars), 454, Pl 13, fig 24), d'Archiac & Haime, 1854 (p 169), Medlicott & Blanford, 1879*b* (p 459)

O (*Gryphaea*) *vesicularis* J de C Sowerby var *nummulitica* Tournouer, in de Bouillé, 1876 (p 40, Pl 7, figs 2, 3)

O (*Gryphaea*) *vesicularis* Lamarck var *globosa* (J de C Sowerby), Fedden, 1880 (p 204)

Gryphaea vesiculosa J de C Sowerby, Newton, in Gregory, 1900 (p 43)

Pycnodonta cf *vesicularis* (Lamarck), L M Davies, 1927 (p 315, table opp p 320), Wadia & L M Davies, 1929 (p 208)

Ostrea archiaci Bellardi MS, d'Archiac, 1850*b* (3, 273)

O archiaci Bellardi, 1852 (pp 262, 295), d'Archiac, in Viquesnel, 1867 (p 457), K Mayer, 1869 (pp 362, 369), Gorizdro, 1915 (pp 44, 51), Petruševskij, 1937 (p 82)

O d'archiaci Bellardi, Sismonda, 1852 (p 324)

O archiaci d'Orbigny, Stache, 1864 (p 88)

O archiaci Bellardi in d'Archiac, d'Archiac in Tchihatcheff, 1866 (p 141)

O archiaci Bronn, C Mayer-Eymar, 1893 (p 20)

O (*Pycnodonta*) *archiaci* Bellardi, Rovereto, 1897 (p 320(11))

Pycnodonta archiaci (Bellardi), Boussac, 1911*a* (pp 180, 408, Pl 9, figs 12, 16), Douvillé, 1920*a* (pp 127, 129, 132), Vialov, 1934*b* (p 47), Bornemann, Buraček & Vialov, 1934 (pp. 257, 259), Jacquet, 1936*a* (p 336), Petruševskij, 1937 (p 82), Flandrin, 1938 (p 145)

Liostrea (*Pycnodonta*) *archiaci* (Bellardi), Cossmann, 1922*a* (p 212, Pl 13, figs 4, 5, 19, 20), Meffert, 1931*a* (p 41, Pl 8, figs 4, 5)

Gryphaea archiaci (Bellardi), Vialov, 1937 (p 1635)

Gryphea archiaci (Bellardi), Vialov, 1936 (p 23)

Ostrea archiaciana d'Orbigny, 1850 (p 327), Cya, 1883 (p 55), Mallada, 1883 (p 55), P E Thomas, 1893 (p 10, Pl 12, figs 4–6), Chautard, 1905 (pp 144, 146)

O (*Pycnodonta*) *archiaciana* d'Orbigny, Chautard, 1905 (p 147, Pl 5, figs 1*a*,*b*,*c*)

O sowerbyana d'Orbigny, 1850 (*non* Bronn, 1836) (p 327)

O (*Gryphaea*) *guembeli* Frauscher, 1886 (p 54, Pl 1, fig 8)

Gryphaea gregoryi Newton, 1905 (p 167, Pl 17, fig 4, Pl 21, figs 1, 2), Oppenheim, 1915 (p 123)

G (*Pycnodonta*) sp ? E Vincent, 1913 (p 26, Pl 2, fig 21)

'*Gryphaea*' L M Davies, 1926*b* (p 205)

Griphaea sp Nicolis, 1886–7 (p 806, Pl 10, fig 2)

References omitted *Ostrea* (*Gryphaea*) *brongniarti* Bellardi, Frauscher, 1886 (Pl 1, figs 11–14, Pl 2, figs 1*a*, 6=*O* (*Pycnodonte*) *frauscheri* Traub, 1938)

Gryphaea (*Pycnodonta*) *brongniarti* Bronn, Desio, 1934 (pp 125, 87, Pl 9, figs 5*a*,*b*, 6*a*,*b*= *Ostrea* (*Liostrea*)(?) sp)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 4) (FB F 1866, *1*), Lower Chocolate Clays (local zone 10) (FB F 1966, *1*, Reg No L 79975), Lower Chocolate Clays (local zone 11/10) (FB F 1968, *10*+), Upper Chocolate Clays (lower part, local zone 12) (FB F 1975, *4*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2552, *2*), White Marl Band (local zone 11) (FB F 2548, *10*+, FB F 2546, *2*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2535, *1*), *Kohat area* (*Panoba section* Lower Shekhan Limestone (local subzone 3*a*) (FB F 2292, *4*), Upper Kohat Shales (local subzone 4*a*) (FB F 2296, *2*), Nummulite Shale (local subzone 4*b*) (FB F 2263, *5*, FB F 2264, *1*, FB F 2266, *7*, FB F 2267, *4*, FB F 2268, *4*), Kohat Limestone (local subzone 4*b*) (FB F 2270, *1*, FB F 2271, *15*+, FB F 2272, *2*, FB F 2273, *2*), Kohat Limestone (local subzone 4*c*) (FB F 2275, *2*), *Kohat area* (*Shekhan Nala section*) Upper Kohat Shales (local subzone 4*a* (FB F 2337, *1*), Nummulite Shale (local subzone 4*b*) (FB F 2345, *15*+, FB F 2346, *15*+, FB F 2347, *15*+, FB F 2349, *6*, FB F 2352, *2*, FB F 2353, *15*+, FB F 2354, *2*), *Kohat area* (*Sirki Paila*) Sirki Shale (local subzone 4*d*) (FB F 2109, *1*), Sirki Shale/Kohat Limestone (local subzone 4*d*) (FB F 2114, *8*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2184, *3*)

Further distribution in India and Pakistan ?Laki of Sind, Laki of the Tochi River district, Nummulite Shales of Kohat, Bahadur Khel, Chharat, and behind Harnai Railway Station, Khirthar of Sukkur-Rohri, the 'Alore Hills' (Sind), and Wage-ke-Pudda (Cutch), Gaj of Cutch (Kotra) and Baluchistan

Further distribution This well-known species has a wide distribution which may be summarized as follows Palaeocene of the Belgian Congo, Landenian of Algeria, Londinian of Switzerland, Lower Eocene of Boukhara, Middle Eocene of Turkey, Algeria, Italy, Somaliland, Tunisia, Asia Minor and southern France, Auversian or Lutetian of Armenia, Auversian of France and Italy, Upper Eocene of Sirtica, Eocene of ?Borneo, Istria, Turkey, northern Spain, the Balkans, Czechoslovakia, Austria, northern Somaliland, Senegal, Arabia, Roumania and south-eastern Afghanistan, Priabonian of Algeria, the Balearic Islands, Boghari (Cyrenaica), the Alps, southern Dagestan, Hungary and Italy, Lower Ligurian of Switzerland, Tongrian of Barrême and Italy, Rupelian of Hungary, southern France and Italy, Chattian of Hungary, Oligocene of Montecchio Maggiore (type locality), the Isle of Rhodes, Hungary, Italy, Haring, Tunisia and Algeria, Schio Beds (Aquitanian) of Italy, and Tertiary of Prechacq, Heugas, Doizit and Bastennes

REMARKS *Gryphaea gregoryi* Newton, from Somaliland, seems to be merely an immature *Ostrea* (*Pycnodonte*) *brongniarti*, similar specimens have been encountered in the Eocene of western Pakistan occurring with and grading into the normal adult form L M Davies's (1925) and Krishnan's (1943) records of *O vesicularis* Lamarck, L M Davies's (1927) and Wadia & L M Davies's (1929) records of *Pycnodonta* cf *vesicularis* (Lamarck), and L M Davies's (1926*b*) record of '*Gryphaea*', from a knowledge of the rocks and fossils of the areas concerned, obviously belong here Frauscher's 1886 record (Pl 1, figs 11-14, Pl 2, figs 1*a*, 6) of *Ostrea* (*Gryphaea*) *brongniarti* Bellardi, from the Middle Eocene of the Bavarian Alps, has been renamed *O* (*Pycnodonte*) *frauscheri* by Traub, 1938 Desio's (1934) record of *Gryphaea* (*Pycnodonta*) *brongniarti* Bronn, from the Eocene of north Africa (pp 125, 87, Pl 9, figs 5*a*, *b*, 6*a*, *b*) is also omitted here, as the illustrations show a form that is apparently an *Ostrea* (*Liostrea*)

Superfamily MYTILACEA

Family MYTILIDAE

Genus *MYTILUS* Linné, 1758

(*Syst Nat* 10th ed , p 704)

TYPE SPECIES *Mytilus edulis* Linne, Recent, Anton, 1839 (Opinion 94 of the International Commission of Zoological Nomenclature indicated that Schumacher's (1817) designation of *Mytilus anatinus* Linné, Recent—an *Anodonta*—as type species of *Mytilus* was overruled)

SYNONYMS *Eumytilus* Jhering, 1900 (*Proc Malac Soc Lond* 4, 86), type species. *M edulis* Linne, Recent, monotypy

MYTILUS NUMMULITICUS d'Archiac & Haime, 1854

REFERENCES *Mytilus indet* d'Archiac, 1850*b* (p 168)

Mytilus nummuliticus d'Archiac & Haime, 1854 (pp 269, 359, 367, Pl 23, fig 12), Fedden, 1880 (p 204), Noetling, 1901 (p 127), Cox, 1931*a* (pp 60, 34)

MATERIAL *Rakhi Nala section* Green and Nodular Shales (local zone 6) FB F 1897,*2*, FB F 1900,*2*, FB F 1903,*2*), Rubbly Limestones (local zone 6) (FB F 1910,*2*, FB F 1912, *1*, FB F 1918,*2*, Reg No L 80198, FB F 2059,*1*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173,*2*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294,*9*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289,*1*, FB F 2291,*4*)

FURTHER DISTRIBUTION IN PAKISTAN Laki of the 'Hala Range' (the type locality)

REMARKS Fedden's (1880) assignation of this species to the Khirthar was made before the Laki Series was established It is possible that Ball's record (1874, p 153) of *Mytilus subcarinatus* Deshayes? from the Eocene of the Luni Pathan Hills, south-east Afghanistan (now in western Pakistan, and possibly of Laki age) may refer to *M. nummuliticus*.

Genus *MODIOLUS* Lamarck, 1799

(*Mem Soc Hist nat Paris*, p 87)

TYPE SPECIES *Mytilus modiolus* Linné, Recent, monotypy

SYNONYMS ?*Volsella* Scopoli, 1771 (*Introd Hist Nat* p 397), type species *Mytilus modiolus* Linné, Recent, Gray, 1847 (*nomen dubium*)

Modiola Lamarck, 1801 (*Syst Anim* p 113), type species *Modiola papuana* (Chemnitz), Recent, monotypy

Eumodiolus Jhering, 1900 (*Proc Malac Soc Lond* 4, 87), type species *Mytilus modiolus* Linné, Recent, monotypy

MODIOLUS DAVIESI Cox, 1931

REFERENCES *Modiolus daviesi* Cox, 1931*a* (pp 61, 28, 34, Pl 3, figs 12, 13*a*, 13*b*)

MATERIAL *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1893, *1*, FB F 1897, *2*), Rubbly Limestones (local zone 6) (FB F 1910, *1*, FB F 1911, *1*, FB F 1912, *1*, FB F 1914, *1*, Reg No L 79976, FB F 1916, *1*), *Kohat area* (*Tarkhobi section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2166, *5*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *7*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *2*), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2293, *1*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294, *7*, Reg No L 79977–83, FB F 2287, *1*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *1*, FB F 2290, *1*, FB F 2291, *3*), *Kohat area* (*Shekhan Nala section*) Middle Shekhan Limestone (local subzone 3*a*) (FB F 2318, *3*)

Accessory samples *Kohat area* (*Tarkhobi*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2193, *1*), Middle Shekhan (local zone 3) (FB F 2180, *1*)

FURTHER DISTRIBUTION IN PAKISTAN Laki of Sind, Shekhan Limestone of Kohat

Genus *MUSCULUS* Bolten, in Roding, 1798

(*Mus Bolt* p 156)

TYPE SPECIES *Musculus discors* (Linné), Recent, Iredale, in Dall, 1915

SYNONYMS *Modiolaria* Beck, in Robert, 1838 (*Zool voy recherche en Islande et en Groenl* p xxviii, Pl 17, figs 1–4), type species *Mytilus discors* Linné, Recent, Stoliczka, 1871

Modiolarca Gray, 1840 (*nomen nudum*), 1847 (*Proc Zool Soc Lond* **15**, 199), type species *Modiola trapezina* Lamarck, Recent, Gray, 1847

Lanistes Swainson, 1840 (*Treat Malac* p 385), *non* Montfort, 1810, type species *Lanistes discors* (Linné), Recent, monotypy

Lanistina Gray, 1847 (*Proc. Zool Soc Lond* **15**, 199), type species *Mytilus discors* Linné, Recent, Gray, 1847

Remarks Some writers have referred to a name *Musculus* Martyn, 1787, and consequently do not use Bolten's generic name The name *Musculus* does not appear in Martyn's work, nor is it quoted from Martyn in Neave (1939–40), consequently the writer follows those authors who use Bolten's name, which appears to be valid

MUSCULUS PUNJABENSIS n sp

(Figures 64*a*, *b*, plate 13)

Material *Rakhi Nala section* Shales with Alabaster (local zone 6) (FB F 1919, the holotype, Reg No L 79984)

Description Shell of moderately small size, not exceedingly thin-shelled, strongly convex, modioliform, distinctly higher posteriorly than anteriorly Umbos well forward, not quite terminal, tumid and prosogyrous, but not projecting Greatest convexity of the shell along the line from the umbo to the postero-ventral corner Antero-dorsal margin very short, gently convex, and moderately descendent Anterior end narrowly rounded Ventral margin long, almost straight, very slightly convex, rather strongly descendent posteriorly Posterior margin gently convex, sloping upwards towards the umbos, joining the ventral margin in a well-rounded curve at the postero-ventral corner, and forming an obtuse angle with the postero-dorsal margin which is long, straight, and horizontal Shell ornamented with radial ribs anteriorly and posteriorly, there being no ribs medially Median band only moderately wide, smooth except for obscure growth lines The anterior portion of the shell carries 14 radial ribs, the posterior four extend progressively shorter distances away from the ventral margin, but this may be due to wear of their dorsal portions, anteriorly, the ribs are broad and wide, rather anadariform, with intervals of about the same width Posterior to the smooth band there are about 18 or 19 radial ribs, rather broad and flat, with intervals a little less or distinctly less than the width of the ribs, the most anterior rib being a little anterior to the sharply rounded portion of the shell running from the umbo to the postero-ventral corner

Dimensions Holotype length (incomplete) 8 0 mm , height 6 2 mm , thickness (one valve) 4 0 mm (approximately) Ratio of length to height according to growth lines 16 9

Remarks The postero-dorsal margin is much straighter, the shell is more transverse, and the rounded angulation extending from the umbo to the postero-ventral corner is more prominent than in *Modiola interstriata* Gumbel as figured by Wolff (1897, p 233, Pl 20, figs 13, 14), from the Oligocene of southern Bavaria The strong inflation and anadariform ribs appear to be characteristic

Subgenus *UNDATIMUSCULUS* n subg

Type species *Musculus* (*Undatimusculus*) *rakhiensis* n sp , Lower Eocene

Subgeneric characters Shell with radial ribs posteriorly, smooth except for growth lines medially, probably ornamented similarly to *Musculus*, with radial ribs anteriorly, but the anterior portion is not preserved Umbonal region with coarse concentric folds

MUSCULUS (*UNDATIMUSCULUS*) *RAKHIENSIS* n sp

(Figure 24, plate 9)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 5) (FB F 1873, the holotype and its impression, Reg No L 79985, and about 5 topotypes, Reg No L 79986–90, some with their impressions)

Description Shell mytiliform in outline, rather flat, only gently convex, of moderate size only Postero-dorsal margin rather long, straight, horizontal Posterior margin slightly convex, obliquely descendent, meeting the postero-dorsal margin in an obtuse angle and the ventral margin in a sharply rounded curve Ventral margin rather straight, ascending anteriorly Anterior portion of shell not preserved Posterior half of shell with 44 fine, flat radial ribs with linear intervals Median portion of shell, the anterior part of which is not preserved, quite smooth except for concentric growth lines In addition to the above ornament there are at least 5 strong, coarse, concentric folds (of *Clementia* type) in the umbonal region

Dimensions Holotype length (incomplete) 11 0 mm , height 9 8 mm

Remarks There seems to be no closely comparable Eogene species, the coarse concentric folds appearing to be unique

Genus *CRENELLA* Brown, 1827

(*Ill Conch Gr Br and Ir* Pl 31, figs 12–14)

Type species *Crenella elliptica* (Leach MS) Brown, Recent = *Mytilus decussatus* Montagu, in Macgillivray, monotypy, and Stoliczka, 1871

Synonyms *Nuculocardia* d'Orbigny, in Sagra, ?1853 (*Hist phys Cuba*, [2], Moll , 2, Fasc 2, p 338, Pl 27, figs 56–59) Type species *N divaricata* d'Orbigny, Recent, monotypy

?*Crenellodon* (Edwards MS) Newton, 1891 (*Syst list F E Edwards Coll Brit Olig and Eoc Moll Brit Mus* p 14)

Remarks The synonymy given by Thiele (1934, p 798) is not followed here It is agreed that *Nuculocardia* falls in synonymy, in spite of the hinge plate being a little more massive and more excavated ventrally *Stalagmium* Conrad, 1833 (*Fossil shells of Tert formations of N America*, p 39), the type species of which is *S margarataceum* Conrad, Eocene, by monotypy, evidently has prosogyrous umbos and a lunule *Hippagus* Lea, 1833 (*Contrib to geol* p 72), the type species of which is *H isocardioides* Lea, Eocene, by monotypy, has very prominent and very strongly prosogyrous umbos and apparently belongs to the Verticordiidae, or elsewhere *Myoparo* Lea, 1833 (*Contrib to geol* pp 73, 74), the type species of which is *M costatus* Lea, Eocene, by monotypy, is less inflated, and has small, distinctly prosogyrous umbos The last three forms are not believed to belong to the genus *Crenella*

CRENELLA ANTERO-DIVARICATA n sp

(Figures 26*a*, *b*, plate 9)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 4) (FB F. 1855, *2*, FB F 1856, *1*, FB F 2023, *3*, Reg No L 79994–6, FB F 1865, *1*), Rubbly Limestones (local zone 6) (FB F 2051, *1*, FB F 1909, *1*), *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 79991, and 2 topotypes, Reg No L 79992–3)

Description Shell oval, very strongly inflated, moderately thick-shelled for its size, higher than wide Umbos more or less erect, slightly prosogyrous, high, rather blunt, submedian Postero-dorsal and antero-dorsal margins steeply descendent, gently convex Posterior and anterior margins convex Ventral margin sharply rounded Ornament consisting of between 60 and 70 fine, flat-topped, moderately prominent, radial riblets which are slightly wider than their intervals There are fewer ribs in the umbonal region, new ones appearing by intercalation and bifurcation Over a cordiform area between the umbo and a position at half the height of the anterior margin, the ribs are more obliquely directed forward so that the rib bounding it has successively more anteriorly placed ribs joining it as it is traced dorsally Internal characters not distinctly seen, but there are definite traces of fairly numerous, fine, transverse crenulations both anterior and posterior to the umbo on the hinge plate

Dimensions Holotype length 2 7 mm , height 3 3 mm , thickness (one valve only) 1 5 mm

Remarks This species has relatively wider interspaces between the ribs compared with *Crenella striatocostata* Nagao (1928, p 46(36), Pl 6, figs 20, 21), from the Palaeogene (Kawamagari Beds) of Japan, and is also broader than the holotype, intercalary ribs are less conspicuous *C cymbiola* Vincent as figured by Glibert (1936, p 37, fig 20), from the Wemmel Sands (Bartonian) of Belgium, is distinctly truncated posteriorly, and seems to have more numerous radial riblets *C scrobiculata* von Koenen (1893, p 1059, Pl 69, figs 1, 2), from the Lower Oligocene of Calbe and Unseburg (north Germany), is broader and has more conspicuous concentric ornament between the riblets *C depontaillieri* Cossmann & Lambert (1884, p 97, Pl 2, figs 12*a*,*b*), from the Oligocene of Jeures, is smaller and narrower, and its riblets are distinctly granulated *C cucullata* Deshayes (1861, p 7, Pl 76, figs 10–12), from the Calcaire Grossier of Grignon and Montmirail, is broader ventrally, the ventral margin not being so convex, and the ornament is finer, the same differences apply to this species as figured by Cossmann & Pissarro (1903, p 21, Pl 3, figs 5, 6), from the Eocene of Hauteville (Cotentin), and as figured by Cossmann & Pissarro (1904*a*, Pl 38, fig 119–3), from the Lutetian of Parnes It is broader and has slightly coarser ornament than *C elegans* Deshayes (1861, p 6, Pl 76, figs 6–9), from the Calcaire Grossier of Grignon, Parnes, Damery, Mouchy, and Chaussy, but is higher, more cardiiform, and with more prominent and more swollen umbos than the same species as figured by Cossmann & Pissarro (1904*a*, Pl 38, fig 119–1), from the Lutetian of Parnes and from the Cuisian *C striatina* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 38, fig 119–2), from the Lutetian of Parnes, is more broadly oval and has somewhat finer ornament *Modiola micans* Al Braun as figured by Speyer (1884, Pl 22, figs 1–6), from the Oligocene of Cassel, is distinctly larger and has finer ornament *Crenella humilis* E Vincent (1930, p 8, fig 3), from the Wemmel Sands (Bartonian) of Belgium, has less numerous radial riblets The oblique anterior riblets of the Pakistan species seem to be unique.

Order HETERODONTA

Superfamily CARDITACEA

Family CARDITIDAE

Genus *VENERICARDIA* Lamarck, 1801

(*Syst An* p 123)

TYPE SPECIES *Venericardia imbricata* Lamarck, Eocene = *Venus imbricata* Gmelin, Schmidt, 1818 and Gray, 1847

SYNONYMS *Pseudocardia* Conrad, 1866 (*Amer J Conch* 2, 103), type species *Venericardia dupiniana* d'Orbigny, Cretaceous, Stoliczka, 1871

Vetocardia Conrad, 1868 (*Amer J Conch* 4, 246) (replacement name for *Pseudocardia*)

Vetericardia Conrad, 1872 (*Proc Acad Nat Sci Philad* (1872), p 52) (amendment of *Vetocardia*)

VENERICARDIA DUFRENOYI (d'Archiac & Haime), 1854

REFERENCES *Cardita dufrenoyi* d'Archiac, 1850*b* (*nomen nudum*) (3, 263), d'Archiac & Haime, 1854 (pp 252, 366, Pl 21, figs 13,*a*), (Fedden, 1880 (p 202), de Bockh, Lees & Richardson, 1929 (p 84), Cox, 1931*a* (pp 69, 34)

DOUBTFUL REFERENCES *Cardita dufrenoyi*, Medlicott, 1864 (p 100)

INCORRECT REFERENCES *Cardita dufrenoyi*, Maureta & Thos y Codina, 1881 (p 321), Mallada, 1883 (p 56), Cya, 1883 (p 56)

MATERIAL *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1924,*1*, Reg No L 79997)

FURTHER DISTRIBUTION IN INDIA AND PAKISTAN The species has been recorded from the Ghazij Shales of the Nilawan Ravine, and from beds probably of Laki age in the 'Hala Range' (the type locality) According to Cox, Medlicott's record of the species from the Khirthar of Subathu is doubtful

REMARKS Mallada's, Cya's and Maureta and Thos y Codina's records of the form from the Eocene of Spain may be disregarded

VENERICARDIA MUTABILIS (d'Archiac & Haime), 1854

REFERENCES *Cardita depressa* d'Archiac & Haime, 1854 (pp 255, 256, Pl 21, figs 1,*a*,*b*, 2,*a*,*b*) *non* Lamarck, 1819 *nec* Munster, 1839, Medlicott & Blanford, 1879*b* (p 531), Blanford, 1880 (pp 119, 127), Fedden, 1880 (p 203), Dollfus, 1915 (p 37), L M Davies, 1925 (p 217)

Venericardia depressa (d'Archiac & Haime), Cossmann & Pissarro, 1927 (p 16, Pl 11, figs 35, 36)

Cardita mutabilis d'Archiac & Haime, 1854 (pp 256, 367, Pl 21, figs 3–6), Medlicott & Blanford, 1879*b* (pp 459, 531), Duncan, 1880 (p 9), Blanford, 1880 (p 48), Fedden, 1880 (p 203), Zittel, 1883 (p 93), Noetling, 1901 (pp 169, 171, 90), Noetling, 1903 (p 514), Noetling, 1905 (pp 133, 134, 137), Cox, 1931*a* (pp 69, 27, 34); Vokes, 1937 (pp 10, 4)

Venericardia mutabilis (d'Archiac & Haime), Douvillé, 1928 (p 22)

Incorrect and doubtful references *Cardita mutabilis* d'Archiac, E Pavay, 1871 (p 367), A von Pavay, 1874 (p 364), Mallada, 1883 (p 56), Cya, 1883 (p 56), Cuvillier, 1930 (pp 133, 166, 266)

C depressa d'Archiac & Haime, Douvillé, 1920*a* (p 128)

C depressa d'Archiac, Cuvillier, 1930 (pp. 133, 166)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1845, *10+*, FB F 1848, *1*, FB F 1849, *2*, FB F 1850, *1*, FB F 1851, *2*, FB F 1852, *4*, FB F 1854, *1*, FB F 1856, *6*, FB F 1860, *6*), Green and Nodular Shales (local zone 5) (FB F 1888, *4*), Rubbly Limestones (local zone 6) (FB F 2054, *1*, FB F 1914, *10+*, FB F 1916, *1*, FB F 1918, *1*), Shales with Alabaster (local zone 6) (FB F 1919, *2*), Shales with Alabaster (local zone 7) (FB F 1931, *2*, FB F 1932, *4*, FB F 1933, *10+*, FB F 1935, *2*, FB F 1936, *10+*, FB F 1937, *10+*, FB F 1938, *6*, FB F 1941, *6*, FB F 1942, *6*, FB F 1943, *10+*), Lower Chocolate Clays (local zone 10) (FB F 1966, *10+*, Reg No L 79998–80003, FB F 1967, *10+*), *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, *2*, FB F 2676, *6*, FB F 2675, *6*), Lower Chocolate Clays (local zone 10) (FB F 2571, *10+*, FB F 2564, *2*, FB F 2562, *6*, FB F 2561, *10+*, FB F 2560, *6*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, *1*, FB F 2537, *1*), *Kohat area* (*Panoba section*) Lower Kohat Shales (local subzone 4*a*) (FB F 2253, *2*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *4*, FB F 2255, *7*, FB F 2295, *2*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *5*, FB F 2257, *15+*, FB F 2297, *4*), *Kohat area* (*Shekhan Nala section*) Upper Kohat Shales (local subzone 4*a*) (FB F 2337, *1*, FB F 2339, *1*, FB F 2340, *1*, FB F 2341, *15+*, FB F 2342, *15+*)

Accessory samples *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *10*, FB F 2184, *15+*)

Further distribution in India and Pakistan Upper Ranikot (zone 4) of Jherruck, and north-west of Kotri, Lower Ghazij Shales from behind Harnai Railway Station, shales of Laki age above Laki Limestone on the Dharan anticline, Middle Subathu (Khirthar) from 22 miles north-west of Simla (and 6 miles west of Arki), Khirthar of Malirı, the Laki Valley, and Subathu (the type locality)

Remarks It seems probable that records from the Middle and Upper Eocene of Egypt and from the Eocene of Senegal are incorrect, since several other Indian and Western Pakistan species recorded from these areas have been shown to be incorrect The records from the Eocene of Spain and Hungary may be neglected

VENERICARDIA SINDENSIS (Cox), 1931

References *Venericardia obliqua* d'Archiac, 1850*b* (*nomen nudum*) (3, 263), Cossmann & Pissarro, 1927 (p 18)

Cardita obliqua (d'Archiac) d'Archiac & Haime, 1854 (pp 251, 366, Pl 21, figs 8, *a*, *b*, *non* Pusch, 1836), Fedden, 1880 (p 202), Dollfus, 1915 (p 37)

C obliqua (d'Archiac) var *subobliqua* d'Archiac & Haime, 1854 (p 252, Pl 21, figs 9, *a*)

C sindensis Cox, 1931*a* (pp 69, 30, 34)

References omitted *Cardita obliqua* (d'Archiac), Garde, 1911 (pp 93, 97, 98, 99, 104, 106, 107, 108)

Material *Rakhi Nala section* Shales with Alabaster (local zone 6) (FB F 1919, *1*), Shales with Alabaster (local zone 7) (FB F 1935, *2*)

Further distribution in western Pakistan Khirthar or Laki of the 'Hala Range' (type locality), Middle Khirthar of the Bugti Hills

Remarks Garde's records of the species from the Eocene of the Soudan are here omitted as they are almost certainly incorrect, several species originally recorded from the Indian subcontinent have been recorded by Garde from Africa, but they are mainly incorrectly identified It seems possible that the *Cardita beaumonti*? d'Archiac recorded by Ball (1874, p 153) from the Eocene of the Luni Pathan Hills might be a *V sindensis* or perhaps a *Venericardia* sp A, *V beaumonti* is a Danian or basal Palaeocene species occurring in horizons older than those containing the fauna recorded by Ball

VENERICARDIA SUBCOMPLANATA (d'Archiac & Haime) 1854

References *Venericardia subcomplanata* d'Archiac, 1850*b* (3, 263, *nomen nudum*)

Cardita subcomplanata d'Archiac & Haime, 1854 (pars) (pp 252, 256, 366, Pl 21, figs 10, 10*a*, *non* fig 11 = *Venericardia*(?) sp), Medlicott & Blanford, 1879*b* (pars) (p 459), Duncan, 1880 (p 9), Blanford, 1880 (pars) (pp 48, 119), Cox, 1931*a* (pp 69, 30, 34), Vokes, 1937 (p 4), Krishnan, 1943 (p 439)

C subcomplanata d'Archiac, Fedden, 1880 (pars) (p 202), Cotter, 1933 (p 97)

Venericardia (*Cardita*) *subcomplanata* d'Archiac, Boettger, 1880 (p 83)

Doubtful records *Cardita subcomplanata* (d'Archiac), Cuvillier, 1930 (p 133)

C subcomplanatus d'Archiac & Haime, Cuvillier, 1930 (p 166)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1966, *2*, Reg No L 80004–5)

Further distribution in Pakistan Khirthar or Laki of Sind, Limestone and shale subdivision of the Upper Chharat in the Attock district, Middle Khirthar of the Bugti Hills, Khirthar of Western Sind The type locality is in the 'Hala Range'

Remarks Records from the Middle Eocene of Egypt must, in view of the fact that several Indian and Pakistan species recorded from Egypt have been found to be incorrectly identified, be regarded as extremely doubtful

VENERICARDIA VREDENBURGI Douvillé, 1929

References *Venericardia vredenburgi* Douvillé, 1929 (pp 65, 71, 72, Pl 10, figs 22–35)

Material *Rakhi Nala section* *Venericardia* Shales (local zone 1) (FB F 1836, *10*+, FB F 1837, *10*+, Reg No L 80006–11)

Further distribution in Pakistan *Cardita beaumonti* Beds of a locality 4 miles west of Ranikot (type locality)

VENERICARDIA PAKISTANICA n sp

(Figures 27*a*, *b*, plate 9)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1842, *2*, FB F 2015, *1*, FB F 1843, *10*+, FB F 1844, *6*, FB F 1849, the holotype, Reg No L 80012, and 8 topotypes, Reg No L 80013–8, FB F 1850, *10*+, FB F 1851, *4*, FB. F 1854, *4*, FB F 2022, *2*, FB F 1855, *1*, FB F 1859, *1*), Green and Nodular Shales (local zone 5) (FB F 1873, *1*, FB F 1890, *10*+), Rubbly Limestones (local zone 6) (FB F. 1910, *1*), Lower Chocolate Clays (local zone 10) (FB F 1966, *1*), *Zinda Pir section* Ghazij Shales (local subzone 3*a*) (FB F 2680, *10*+, FB F 2679, *6*), Ghazij Shales (local subzone 3*b*) (FB F 2675, *2*)

Description Shell of moderately small size, oval-subtriangular, moderately strongly inflated when not squashed during fossilization Umbos small, only moderately prominent, pointed, prosogyrous, situated anterior to the median line at about two-fifths of the length Outline suborbicular except for the umbos, ventral margin less convexly rounded than the ends, posterior end in some of the squashed specimens with its outline somewhat truncated obliquely There are 19 square-topped ribs which are slightly wider than their intervals, but which have strong, closely spaced, rounded or slightly transverse beads which give them a superficial appearance of being slightly narrower than their intervals

Dimensions Holotype length 14 0 mm, height 12 7 mm, thickness (both valves) 8 7 mm

Remarks *Venericardia subcomplanata* (d'Archiac & Haime) is larger, has more anteriorly situated umbos, and has slightly more numerous ribs (22, as against 19 in *V pakistanica*) *V subcomplanata* (d'Archiac & Haime) var d'Archiac & Haime (= *Venericardia*(?) n sp) is more carditform *V yoshidai* Nagao (1928, p 57(47), Pl 12, figs 14, 15), from the Itanoura Beds and Kishima Beds of Japan, is larger, has 21 to 23 ribs, and is till more orbicular

VENERICARDIA SORIENSIS n sp

(Figures 65*a*, *b*, *c*, *d*, plate 13)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, the holotype, Reg No L 80019)

Description Shell of moderately small size, suborbicular-subquadrate, moderately strongly inflated Umbos small, distinct, not very prominent, prosogyrous, situated anterior to the middle line at about five-sevenths of the length Antero-dorsal margin very short, gently convex, moderately descendent Anterior end rounded Ventral margin gently convex, the curvature rather flattened Posterior end rounded, with indications of a vague truncation on its upper portion Postero-dorsal margin moderately long, fairly straight, gently descendent There are about 23 fine, V-shaped radial ribs with shallow, U-shaped intervals which are distinctly wider than the ribs The ribs carry small, rather widely spaced, regular, forwardly projecting, scaly spines which, on the ventral margin, may be about 1 mm apart

Dimensions Holotype length 14 3 mm, height 12 4 mm, thickness (both valves) 8 5 mm

Remarks The outline is much the same as in *Cardita aegyptiaca* Fraas as figured by Dareste de la Chavanne (1910*a*, p 8, Pl 1, figs 9*a*–*g*), from the Eocene of Guelma, but the ribbing is not definitely tripartite and the intervals between the ribs appear wider *Venericardia carinata* J Sowerby as figured by Glibert (1933, p 137, Pl 8, fig 4), from the Bruxellian of Neder-Ockerzeel (Belgium), is distinctly larger, is more elongate, and has much more closely spaced scaly spines on the ribs. *Cardita* (*Venericardia*) *miqueli* Doncieux

(1911, p 80, Pl 9, fig 14), from the Lower Lutetian of Coustouge (vallon du Scié), is more strongly inflated, has larger and more prominent umbos, and has a more excavated lunular region

VENERICARDIA TRACHYCARDIIFORMIS n sp

(Figures 66*a*, *b*, *c*, *d*, plate 13)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2541, *2*, FB F 2539, the holotype, Reg No L 80020)

Description Shell of only moderate size, strongly inflated, higher than wide, oval in outline Umbos prominent, swollen, prosogyrous, situated a little anterior to the middle line Except for the umbos, the outline is oval There are 24 or 25 fine, sharp, V-shaped radial ribs which have rather wide, U-shaped intervals, they are not very well preserved, and any ornament they may have carried has been destroyed

Dimensions Holotype length 12 2 mm , height 13 8 mm , thickness (both valves) 9 8 mm

Remarks *Cardita zitteli* Cuvillier (1930, p 308, Pl 16, figs 12, 13), from the Upper Mokattam of Egypt, has only 15 to 16 ribs and, although the outline is similar, the Egyptian species is still more strongly inflated *Venericardia tumida* von Koenen var *dujeprovensis* Slodkevich (1933, p 20, Pl 3, figs 8–14), from the Palaeogene of Mandrykovka (Russia), has a somewhat similar outline, but is a little smaller, not quite so high, and has coarser ribbing *V vicinalis* Leymerie (1846, p 362, Pl 15, fig 9), from the Eocene of Saint-Laurent (Corbières), is a little larger, has less swollen and less conspicuous umbos, is less cardiiform, and apparently has about two more ribs *V squamosa* Lamarck as figured by Vasseur (1917, Pl 16, figs 17–22), from the Eocene of Bois-Gouet, is distinctly less high, and has noticeably coarser ornament

Subgenus *PTEROMERIS* Conrad, 1862

(*Proc Acad Nat Sci Philad* (1862), p 290)

Type species *Cardita perplana* (Conrad), Miocene = *Venericardia radians* Conrad, original designation

Synonyms *Coripia* de Gregorio, 1885 (*Bull Soc malac Ital* **10**, 153), type species *Cardita* (*Coripia*) *corbis* Philippi, Pliocene-Recent, monotypy

Triodonta von Koenen, 1893 (*Abh geol Spezialk Preussen*, **10**, 1209) *non* Bory de St Vincent, 1827 (Prot) *nec* Mulsant, 1842 (Col) *nec* Agassiz, 1846 (Moll) *nec* Williston, 1885 (Dipt) Examples *Cardita corbis* Philippi, Pliocene—Recent, *Triodonta clara* von Koenen, Lower Oligocene, *Triodonta deleta* von Koenen, Lower Oligocene

Miodon auct

VENERICARDIA (*PTEROMERIS*) (?) *UMBONIPERDITA* n sp

(Figures 67*a*, *b*, plate 13)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2730, the holotype, Reg No L 80021)

Description Shell suborbicular in outline, a little more sharply rounded ventrally, slightly truncated postero-ventrally, small Umbos broken, but the adjacent marginal outline suggests that they were probably prosogyrous and submedian in position Moderately strongly inflated Surface ornamented with radial ribs of which there are about 35 at the margins of the shell, a few of these having originated by intercalation at a late stage of growth, others by bifurcation at various stages, the ribs are gently rounded, apparently not beaded, broad, with narrow intervals, and are sharper and narrower in the young stages

Dimensions Holotype length 1 3 mm , height 1 3 mm , thickness (both valves) 0 94 mm

Remarks This species is only provisionally placed as a *Pteromeris*, forms referred to this subgenus being usually less inflated and having simple unbifid ribs with no intercalaries In form it resembles several species of *Pteromeris* recorded from the Palaeogene of France, all of which , however, have simple ribbing *P barrandei* (d'Archiac) as figured by Cossmann (1922*a*, p 124, Pl 7, figs 18–25), from the Bartonian of the Côte des Basques (Biarritz) and from the Auversian of 'Lady Bruce' (Biarritz), is larger and has distinctly beaded ribs *P meridionalis* Cossmann (1922*a*, p 125, Pl 7, figs 41–44), from the Stampian of Sarcignan and Caudéran, has more conspicuous and strongly beaded ribs *P sacyi* Cossmann (1922*a*, p 126, Pl 7, figs 50, 51), from the Stampian of Caudéran, has stronger and distinctly beaded ribs

The form illustrated by Speyer (1884, Pl 15, fig 8), from the Chattian of Hohenkirchen, as *Woodia beyrichi* is somewhat similar, but is higher and has more distinct ornament, *Woodia* is a synonym of *Digitaria*, but Speyer's form is not a *Digitaria*

VENERICARDIA sp A

(Figures 68*a*, *b*, plate 13)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1897, the holotype, Reg No L 80022)

Description Shell of moderately large size, rather strongly inflated, transversely oval-subtriangular Umbos small, swollen, moderately prominent, distinctly prosogyrous, situated anterior to the median line at about fifteen-seventeenths of the length Postero-dorsal margin more or less straight, moderately long, moderately descendent Posterior end moderately narrowly rounded Ventral margin moderately convex Anterior end high, broadly rounded Antero-dorsal margin slightly convex, rather short, steeply descendent There were probably about 25 ribs, but the preservation is too poor for their number or characters to be determined

Dimensions Holotype length 25 7 mm , height 22 8 mm , thickness (both valves) 18 4 mm

Remarks *Venericardia sindensis* (Cox) is smaller and less inflated The holotype is very similar to fig 11 of *Cardita mandaica* Yokoyama (1911, p 9, Pl 2, figs 8–11), from the Miike Coal-Field Eocene of Japan, but Yokoyama's figs 8–10 are distinctly more trapezoidal The species is more inflated than any of d'Archiac & Haime's species except *Venericardia beaumonti*, which is still more strongly inflated The transversely oval outline and rather forwardly placed umbos appear to be characteristic

VENERICARDIA sp B

(Figures 25*a*,*b*,*c*, plate 9)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F. 1897,*1*, FB F 1900, the holotype, Reg No L 80023, and 3 topotypes, FB F 1902, *1*), Shales with Alabaster (local zone 7) (FB F 1923,*6*, FB F 1934,*1*, FB F 1935,*4*)

Description Shell oval-suborbicular to somewhat subtrapezoidal in outline, moderately strongly inflated Umbos small, pointed, prosogyrous, situated well anterior to the median line at about seven-eighths of the length Postero-dorsal margin gently convex, not very long, little descendent Posterior end high, convexly rounded Ventral margin not very long, rather gently convex Anterior end moderately convex, high Surface more strongly arched between the umbos and the postero-ventral corner There were at least 25 fine, sharp, thread-like riblets which, on the specimen illustrated, appear to be separated by broad U-shaped intervals

Dimensions Holotype length 18 7 mm , height 18 6 mm , thickness (both valves) 13 2 mm

Remarks *Venericardia ovoides* d'Archiac & Haime has less numerous ribs with, apparently, still wider intervals, and is less orbicular *V subcomplanata* (d'Archiac & Haime) var d'Archiac & Haime (= *Venericardia* n sp.) is also similar, but the ribs are more widely spaced and the outline is rather different

Superfamily Lucinacea

Family Ungulinidae

Genus *DIPLODONTA* Bronn, 1831

(*Ergebn nat Reisen*, 2, 484)

Type species *Venus lupinus* Brocchi (*non* Linné), Miocene-Pliocene = *Tellina rotundata* Montagu var *aequilateralis*, Herrmannsen, 1847 and Gray, 1847

Synonyms ? *Taras* Risso, 1826 (*H N Europe*, 4, 344), type species *T antiquatus* Risso, Recent, monotypy (*nomen dubium*)

Mysia (Leach) Brown, 1827 *non* Lamarck, 1818 (*Ill Conch G B and I* Pl 16, fig 11), type species *M rotundata* (Montagu), Recent, monotypy

Glocomene Leach, in Gray, 1852 (*Moll Brit Syn* p 313), examples *G montaguana* Leach, in Gray, Recent, *Tellina rotundata* Montagu, Recent, *T undata* Pulteney, Recent

Cycladicama Valenciennes, in Rousseau, 1854 (*Voy Pôle Sud*, 5, 116), type species *C luciniformis* Valenciennes, in Rousseau, Recent, monotypy

Mittrea Gray, 1854 (*Ann Mag Nat Hist* (2) 14, 25), type species *Diplodonta brasiliensis* Mittre, Recent, original designation and monotypy

DIPLODONTA HINDU Cox, 1931

References *Diplodonta hindu* Cox, 1931*a* (pp 78, 28, 34, Pl 3, figs 20*a*,*b*, 21, 22)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1900,*1*), Shales with Alabaster (local zone 6) (FB F 1919,*1*), Shales with Alabaster (local zone 7)

(FB F 1930, *1*, FB. F 1931, *12*, Reg No L 80024–9, FB F 1932, *10*+, FB F 1934, *1*, FB F 1935, *10*+, FB F 1937, *1*), *Kohat area* (*Panoba section*) Upper Shekhan Limestone (local subzone 3*b*) (FB F 2291, *2*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *1*)

Further distribution in Pakistan Laki of Sind (a doubtful cast), Ghazij Shales of Hindu Bagh (the type locality).

DIPLODONTA INDICA Cox, 1931

References *Mactra dubia* d'Archiac, 1850*b* (3, 257, *nomen nudum*), L M Davies, 1926*c* (p 247)

Mactra dubia d'Archiac & Haime, 1854 (pp 233, 240, 365, Pl 16, figs 12,*a*) *non* J Sowerby, 1817, Fedden, 1880 (p 201)

Diplodonta (?) *indica* Cox, 1931*a* (pp 78, 34)

Doubtful references *Mactra dubia* d'Archiac, Gorizdro, 1915 (pp 36, 43, 50)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1900, *1*), Shales with Alabaster (local zone 7) (FB F 1930, *1*, FB F 1931, *10*+, Reg No L 80030–5, FB F 1932, *10*+, FB F 1934, *2*, FB F 1935, *10*+, FB F 1937, *1*, FB F 1954, *6*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *2*), *Kohat area* (*Panoba section*) Upper Shekhan Limestone (local subzone 3*b*) (FB F 2291, *1*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *1*)

Further distribution in Pakistan Eocene (? Ghazij Shales) of Hindu Bagh, probably Laki of the 'Hala Range', Sind (type locality)

Further distribution The record from the Eocene of Turkestan is unaccompanied by illustrations and is therefore to be regarded as somewhat doubtful

Remarks As Cox has remarked, the general appearance of this species recalls *Diplodonta* rather than *Mactra* The Rakhi Nala specimens have no pallial sinus, and there consequently appears to be no necessity to query the generic identification

DIPLODONTA PAKISTANICA n sp

(Figures 69*a*, *b*, *c*, plate 13)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1966, *10*+, FB F 1967, the holotype, Reg No L 80036, and 11 topotypes, Reg No L 80037–42), White Marl Band (local zone 11) (FB F 1970, *1*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2570, *2*, FB F 2558, *2*, FB F 2733, *10*+, FB F 2555, *2*, FB F 2565, *2*, FB F 2554, *2*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2184, 2)

Description Shell of fairly large size for the genus, suborbicular-subquadrate in outline, thin-shelled, inflation moderate Umbos small, distinct, pointed, erect, situated slightly anterior to the median line Antero-dorsal margin steeply descendent, gently convex, merging imperceptibly with the gently convex anterior end which slopes upwards towards the umbos Ventral margin moderately convex, the antero-ventral margin being a little produced and more sharply rounded than the anterior and ventral margins Posterior end vaguely truncated, slightly to gently convex, sloping upwards towards the umbos, meeting the ventral margin in a curve which is less sharply rounded than that of the antero-ventral margin, and meeting the postero-dorsal margin in an obtuse angle Postero-dorsal margin fairly straight, of moderate length, gently descendent Surface smooth except for irregularly accentuated growth lines Valve margins internally smooth Lunule absent Posteriorly on the dorsal margin the escutcheon shows as a narrow, subcordiform depressed area which is about half as long as the postero-dorsal margin Internal moulds show two raised ridges in a similar position anterior to the umbos, limiting a slightly larger area than the escutcheon No pallial sinus There is some variation in relative proportions, the umbos sometimes being more forwardly situated, the antero-ventral or postero-ventral regions, or both, being more produced, or the shell may be still more orbicular than the holotype, in spite of this variation the general appearance and size remain readily recognizable The region between the umbos and the postero-ventral corner is a little more strongly inflated than the rest of the shell

Dimensions Holotype length 33 4 mm , height 31 0 mm , thickness (both valves) 14 0 mm

Remarks *Diplodonta indica* is normally not quite so large, and is less quadrate in outline than *D pakistanica*, the size and shape of which appear to be characteristic There is a close superficial resemblance between *D pakistanica* and *Cyrena quadrangularis* Oppenheim (1901 *b*, p 246, Pl 15, fig 6), from the Eocene of the Balkans, but the latter form is a little smaller, has a more vertical posterior truncation, and is, moreover, thick-shelled

DIPLODONTA SORIENSIS n sp

(Figures 70*a*, *b*, plate 13)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2558, the holotype, Reg No L 80043, and 3 topotypes, Reg No L 80044–6, FB F 2557, *2*, FB F 2733/2550, *10*+, FB F 2569, *1*, FB F 2567, *1*, FB F 2554, *2*, FB F 2563, *2*, FB F 2553, *2*, FB F 2731, *2*, FB F 2551, *1*, FB F 2730, *1*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2539, *1*)

Description Shell of moderate size, parallelepipedic in outline, moderately strongly inflated Greatest inflation along the line from the umbos to the postero-ventral corner Umbos small, not prominent, situated anterior to the median line at between one-third and one-quarter of the length Postero-dorsal margin horizontal, straight, not long Posterior end truncated, the truncation being oblique on the holotype but almost vertical on one of the topotypes, the margin being straight to very slightly convex in outline, meeting the postero-dorsal margin in a rounded obtuse angle which is greater in the holotype than in the topotype mentioned above, meeting the ventral margin in a rounded curve Ventral margin almost straight, parallel to the postero-dorsal margin Anterior end short, convexly rounded, merging imperceptibly with the antero-dorsal margin which is very slightly convex, rather short, and steeply to very steeply descendent Shell apparently smooth except for obscure growth lines, the valve margins appearing to have been smooth internally There is a narrow, lanceolate escutcheonal depression posterior to the umbos and occupying most of the length of the postero-dorsal margin

Dimensions Holotype length 22 1 mm , height 21 9 mm , thickness (both valves) 11 4 mm Topotype length 18 7 mm , height 21 1 mm , thickness (both valves) 11 2 mm

Remarks The specimens are nearly all moulds The markedly parallelepipedic outline appears to be characteristic The obliquity of the posterior truncation is apparently a variable character, but the parallel postero-dorsal and ventral margins give a characteristic appearance to the species

DIPLODONTA(?) *PUNJABENSIS* n sp

(Figures 71*a*,*b*, plate 13)

Material *Zinda Pir section* White Marl Band (local zone 11) (FB F 2734, the holotype, Reg No L 80047, and 5 topotypes, Reg No L 80048–52)

Description Apparently thin-shelled, appearing to have been smooth except for incrementals, lunular and escutcheon areas obscured by matrix Shell transversely oval-subrectangular, rather strongly inflated Umbos not large, prosogyrous, situated anterior to the middle line at about one-third of the length of the shell Antero-dorsal margin not long, slightly convex, moderately steeply descendent Anterior end rounded Ventral margin subhorizontal, gently convex, joining the anterior and posterior ends in a broadly rounded curve Posterior end rounded, with some indication of a very slight truncation Postero-dorsal margin rather long, fairly straight, gently descendent Valve margins apparently smooth internally Pallial sinus absent The posterior area shows signs of a vague flattening as in *Diplodonta* Some specimens tend to be more elongate

Dimensions Holotype length 32 8 mm , height 26 2 mm , thickness (both valves) 17 8 mm Topotype length 37 6 mm , height 26 0 mm , thickness (both valves) 20 4 mm

Remarks The specimens are all moulds The species is referred tentatively to the genus *Diplodonta* on account of the nearly smooth, inflated nature of the shell, and because of the presence of a vague posterior area, any resemblance to the genus *Anodontia* is deceiving, the umbos being too forwardly placed It superficially resembles *Crassatellites fuscus* Yokoyama as figured by Nagao (1928, p 107(11), Pl 18(1), figs 7, 7*a*), from the Manda Group (Palaeogene) of the Miike coal-field, Japan, but the antero-dorsal margin is not excavated *Diplodonta hindu* Cox (1931*a*, p 78, Pl 2, figs 20*a*, *b*, 21, 22), from the Ghazij Shales of Hindu Bagh and the ?Laki of Sind, is not so large and is considerably less transverse

DIPLODONTA sp A

(Figures 72, 73, plate 13)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2556, the holotype, Reg No L 80053, and 1 topotype, Reg No L 80054, both badly preserved moulds)

Description The holotype, which is crushed in from behind, is oval-subtriangular in shape, with high, prominent umbos situated far forward at less than a quarter of the length of the shell Anterior end short and broadly rounded, merging insensibly into the antero-dorsal margin which is short, slightly convex, steeply descendent Ventral margin almost straight, horizontal Posterior end crushed in, but the postero-ventral corner appears to be drawn out, giving a triangular appearance to the outline Inflation rather strong, especially along the line from the umbos to the postero-ventral corner, but this is probably due in part to crushing The topotype is much less strongly inflated and more oval in outline Posterior end vaguely and obliquely truncated, gently convex in outline, rising upwards obliquely towards the umbos to meet the moderately short, straight, horizontal postero-dorsal margin in a very rounded obtuse angle Ventral margin gently convex Anterior end moderately rounded Antero-dorsal margin almost straight, short, steeply descendent Both specimens appear to have been smooth

Dimensions Holotype length 25 0 mm , height 23 2 mm , thickness (both valves) 14 4 mm Topotype length 21 5 mm , height 19 5 mm , thickness (both valves) 9 4 mm

Remarks These specimens may be crushed and ill-preserved *Diplodonta soriensis*, although the differences exhibited are considerable The smaller specimen is narrower and still more oblique than *Taras* (*Felaniella*) *wemmelensis* Glibert (1936, p 110, Pl 3, fig 11), from the Wemmel Sands (Bartonian) of Neder-over-Heembeek, Belgium

Family Lucinidae

Genus *LUCINA* Bruguière, 1797

(*Ency Méth* (*Tabl Vers*), Pl 284)

Type species *Lucina pensylvanica* (Linné), Recent = '*Venus*' *pensylvanica* Chemnitz, Schmidt, 1818

Synonyms *Egraca* Leach, in Gray, 1852 (*Moll Brit Syn* p 310), type species *idem* (= *Lucina*)

Linga de Gregorio, 1885 (*Bull Soc malac Ital* **10**, 217), type species quoted as being *Lucina columbella* Lamarck, Miocene

Remarks The author does not agree with Chavan's (1937–8, **81**, no 2, pp 134–142) conclusions as to the authorship and type species of *Lucina* Although Bruguière did not give any description of his genus or species, the interpretation of the species figured by him is undisputed According to the International Rules of Zoological Nomenclature, this is sufficient to establish the genus Of the type designations that are usually quoted, Schumacher (1817, pp 164–165) referred to *Lucina* Lamarck, and did not mention a type, Anton (1839, p 6), although recording in his introduction that the first species under all genera was printed in italics to indicate that it was the type, divided *Lucina* Bruguière into four groups, the first species in each group being printed in italics—thus invalidating all of them, and Herrmannsen (1846–7, pp 628–630) referred to *Lucina* Bruguière, 1792, and to *Lucina* Schumacher The earliest valid type designation seems to be that of Schmidt (see Winckworth, 1944, p 23)

LUCINA METABLETA Cossmann, 1901

References *Lucina metableta* Cossmann, 1901 *b* (p 195(25), Pl 3, figs 11–13), Oppenheim, 1903 *a* (p 133, Pl 13, figs 9–11), Blanckenhorn, 1921 (pp 86, 88, 93, 96), Cuvillier, 1930 (pp 122, 123, 133, 167, 205, 215, 218, 222, 268), Cox, 1931 *a* (pp 72, 33, 34, Pl 4, fig 2), Brown, 1931 (p 267), Cox, 1936 (pp 32, 7, Pl 4, fig 3), Furon, 1941 (p 335), Borooah, 1946 (p 317)

MATERIAL *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1893, *10*+, FB F 1899, *1*, FB F 1901, *10*+, FB F 2042, *1*, FB F 1902, *1*, FB F 1903, *1*), Rubbly Limestones (local zone 6) (FB F 1904, *6*, FB F 2049, *1*, FB F 1910, *1*, FB F 1911, *2*, FB F 1915, *2*, FB F 1916, *1*, FB F 1917, *10*+, FB F 1918, *1*), Shales with Alabaster (local zone 6) (FB F 1919, *6*), Shales with Alabaster (local zone 7) (FB F 1932, *1*, FB F 1935, *2*, FB F 1941, *1*, FB F 1943, *4*, FB F 1948, *2*), Lower Chocolate Clays (local zone 10) (FB F 1966, *10*+, FB F 1967, *1*, Reg No L 80055), Lower Chocolate Clays (local zone 11/10) (FB F 1962, *1*), *Zinda Pir section* Ghaziji Shales (local subzone 3*a*) (FB F 2679, *2*), Lower Chocolate Clays (local zone 10) (FB F 2570, *1*, FB F 2558, *10*+, FB F 2557, *6*, FB F 2555, *10*+, FB F 2569, *2*, FB F 2567, *1*, FB F 2732, *1*, FB F 2564, *6*, FB F 2731, *1*, FB F 2552, *1*, FB F 2730, *2*), *Kohat area* (*Tarkhobi section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2159, *2*, FB F 2161, *4*, FB F 2163, *15*+, FB F 2164, *4*, FB F 2166, *7*), Middle Shekhan Limestone (local subzone 3*a*) (FB F 2168, *5*, FB F 2169, *7*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, *15*+, FB F 2172, *2*, FB F 2173, *15*+), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *15*+), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2292, *15*+, FB F 2293, *15*+, FB F 2224, *2*, FB F 2225, *1*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2228, *2*, FB F 2230, *15*+, FB F 2294, *15*+, FB F 2231, *1*, FB F 2287, *15*+), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *15*+, FB F 2290, *4*, FB F 2291, *15*+), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *1*), *Kohat area* (*Shekhan Nala section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2319, *1*), Upper Kohat Shales (local subzone 4*a*) (FB F 2338, *1*, FB F 2341, *1*, FB F 2342, *1*)

Accessory samples *Kohat area* (*Tarkhobi*) Tarkhobi Shales (*Irregularis* Bed, local zone 2) (FB F 2186, *1*), Tarkhobi Shales (25 ft above *Irregularis* Bed, local zone 2) (FB F 2188, *1*), Lower Shekhan Limestone (local subzone 3*a*) (FB F 2193, *4*, FB F 2194, *1*, FB F 2196, *3*), Middle Shekhan (local zone 3) (FB F 2180, *2*), Kohat Shales (local subzone 4*a*) (FB F 2183, *3*, FB F 2184, *2*)

FURTHER DISTRIBUTION IN INDIA AND PAKISTAN Laki of Nagurda (about 20 miles north of Kapurdi, Jodhpur State), Laki of Saidpur (Hyderabad District, Sind)

FURTHER DISTRIBUTION Lower Mokattam of Egypt (type locality), Middle Eocene of Somaliland and Bahrein Island, Upper Mokattam of Egypt

LUCINA RAKHIENSIS n sp

(Figures 81*a*, *b*, plate 14)

MATERIAL *Rakhi Nala section* Rubbly Limestones (local zone 6) (FB F 1915, the holotype, Reg No L 80056, and 18 topotypes, Reg No L 80057–63), Shales with Alabaster (local zone 7) (FB F 1929, *4*, FB F 1939, *1*)

DESCRIPTION Shell of only moderate size, moderately strongly inflated, suborbicular in outline when not distorted, distortion often producing specimens that are more strongly inflated than usual and which are higher than wide Umbos moderately small, not projecting much, situated slightly anterior to the median line Antero-dorsal margin not long, slightly convex, gently descendent Anterior end rather sharply rounded Ventral margin fairly strongly convex. Posterior end truncated, almost straight, high, meeting the ventral margin in a sharply rounded curve and the postero-dorsal margin in a blunt, rounded angle of a little more than 90° Postero-dorsal margin moderately long, straight, gently descendent Anterior area obscure, evidently restricted to a small portion of the surface anterior to the umbos and delimited by incised lines on the moulds Posterior area large, slightly concave, limited by a blunt but variable carination of the surface, and extending from the umbo to the postero-ventral corner Ornament consisting of thin, sharp, distinct, widely spaced concentric lamellae of which there are 3 in 1·07 mm near the ventral margin medially, and which become obsolete on the posterior part of the posterior area On some specimens the threads become weaker close to the ventral margin, and are there mingled with closely spaced concentric threads of the same strength

Dimensions Holotype length 11 0 mm , height 9 2 mm

Remarks *Lucina metableta* Cossmann is considerably larger and higher *Lucina narica* Vredenburg, from the Lower Nari of the north-eastern Takatu Range, Baluchistan, is more transverse, less truncated posteriorly, and has a less concave posterior area and a less distinctly straight dorsal margin The form, sharp, widely spaced ornament, and relatively small size seem to be characteristic

LUCINA EXQUISITA n sp

(Figures 74*a*,*b*, plate 13)

Material *Zinda Pir section* Ghazij Shales (local subzone 3*a*) (FB F 2679, the holotype, Reg No L 80064, and 1 topotype, Reg No L 80065)

Description Shell of moderately small size, subtriangular with a convex ventral margin, tending to be cuneiform anteriorly, with distinct areas, very solid and thick-shelled for its size, moderately inflated Umbos small, prominent, prosogyrous, submedian in position Antero-dorsal margin moderately long, slightly concave, rather steeply descendent Anterior end bluntly pointed Ventral margin strongly convex, with a fairly small emargination near the anterior end where the furrow limiting the anterior area meets it Posterior end vertical as a whole, deeply concave, short, its lower limit coinciding with the line of demarcation of the posterior area Postero-dorsal margin moderately long, moderately convex, only slightly descendent near the umbo, becoming fairly steeply descendent posteriorly Ornament consisting of strong, coarse, widely spaced, prominent, concentric lamellae which are about 1 mm apart on the median part of the shell, but become a little more closely spaced near the ventral margin Anterior area not well marked in youth, narrowly triangular, limited in the adult by a relatively broad radial furrow meeting the ventral margin near its anterior end Posterior area luciniform, abruptly sunk adjacent to the line limiting it anteriorly, its posterior half inflated again like the main portion of the shell, the line limiting it anteriorly is slightly convex towards the postero-dorsal margin in the young stages, but straight and very steeply descendent in the adult Lunule a large, sunken, flattened, narrowly cordiform area occupying the whole space between the umbos and the anterior end, ornamented solely with sharp, irregular, raised growth lines Escutcheon indistinct, consisting of a relatively short, narrow, deeply depressed area just posterior to the umbos

Dimensions Holotype length 9 1 mm , height 8·0 mm , thickness (both valves) 5 3 mm.

Remarks *Lucina prae-orbicularis* Tournouer (1873, p 468, Pl 8, fig 8), from the *Serpula spirulaea* sands of Peyrehorade, has much less prominent umbos and a distinctly less steeply sloping antero-dorsal margin

Subgenus *BELLUCINA* Dall, 1901

(*Proc U S Nat Mus* **23**, 806)

Type species *Parvilucina eucosmia* Dall, Recent = *Lucina pisum* Reeve, 1850 *non* Sowerby, 1837 = *Bellucina semperiana* Issel, original designation

Synonym *Cardiolucina* Sacco, 1901 (*I Moll terr terz Piem e Lig* **29**, 89), type species *Cardium agassizii* Michelotti, Miocene, original designation

Remarks Chavan's (1937–38, **81**, no 3, p 205) views as to the synonymy are adopted

LUCINA (*BELLUCINA*) *PRAEAGASSIZI* n sp

(Figures 82*a*, *b*, plate 14)

Material *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 13) (FB F 2520, the holotype, Reg No L 80066, FB F 2519, 2)

Description Shell small, transversely oval, thick-shelled for its size Umbos small, not very pointed, distinct, prosogyrous, situated posterior to the middle line at about four-ninths of the length Antero-dorsal margin of moderate length, concave near the umbos, thence gently convex and becoming gently descendent distally Anterior end well rounded, appearing slightly produced Ventral margin gently convex, subhorizontal as a whole Posterior end truncated, straight, sloping upwards slightly away from the umbos, of moderate length, joining the adjacent ventral and postero-dorsal margins in well-rounded obtuse angles Postero-dorsal margin of moderate length, slightly convex, fairly steeply descendent No anterior area Posterior area indistinct, consisting of a very shallow concave area between the posterior end, the postero-dorsal margin and a line joining the umbo to the postero-ventral corner Ornament consisting of strong concentric lamellae and fine intercalary radial threads In the young stages the concentric lamellae are of about the same width as their intervals, but in the adult they may be more widely spaced, although the last two are very close together, there are about 5 lamellae in ¾ mm in the adult, although at three stages there are extra-wide intervals, the latest one being the widest and attaining a width of 0 375 mm Intercalary radial threads not very well preserved, but appearing to be a little wider than their intervals, there are about 8 in ¾ mm From the appearance of the ventral margin, the valve margins were crenulated internally Lunule a short, almost circular, deeply sunken pit just anterior to the umbos Escutcheon a short, narrow, lanceolate, deeply sunken area just posterior to the umbos and extending for about half the length of the postero-dorsal margin

Dimensions Holotype length 2 34 mm , height 2 0 mm , thickness (both valves) 1 56 mm.

Remarks *Cardiolucina agassizi* (Michelotti) as figured by Sacco (1901, p 89, Pl 20, figs, 37–39), from the Tortonian and Helvetian of Italy, *C agassizi* (Michelotti) var *regularior* Sacco (1901, p 90, Pl 20, figs 40–42), from the Tortonian and Helvetian of Italy, and

C aggassizi (Michelotti) var *constricta* Sacco (1901, p 90, Pl 20, fig 43), from the Helvetian of Italy, are all less transversely oval and the concentric lamellae are on the whole finer and more regularly disposed While Cossman & Peyrot's (1911, p 325, Pl 28, figs 83–86) illustrations of *Phacoides* (*Cardiolucina*) *agassizi* (Michelotti), from the Tortonian and Helvetian of France, show three zones where the concentric lamellae have an abnormally wide interval, the specimens are nevertheless much less transverse and more drawn out antero-ventrally than *Lucina* (*Bellucina*) *praeagassizi* *Phacoides* (*Parvilucina*) *ligatus* Cossmann & Pissarro (1904*b*, p 17, Pl 6, figs 1–4), from the Eocene of Hauteville, is also a higher and distinctly less transverse form

Genus *PHACOIDES* (Blainville) H & A Adams, 1858

(*Gen Rec Moll* **2**, 467)

Type species *Lucina jamaicensis* Spengler, Recent monotypy

Synonyms '*Les L Phacoides*' Blainville, 1825 (*Dict Sci Nat* **32**, 334), a vernacular name (Sole example *Lucina jamaicensis* Spengler)

Phacoides Agassiz, 1845 (*Nom Zool* (*Moll*), **2**, 67), name without species (a quotation from Blainville)

Dentilucina Fischer, 1887 (*Man Conch* p 1143), type species *Lucina jamaicensis* Lamarck, Recent, monotypy

Remarks The acceptance of *Lucina pennsylvanica* (Linné) as the type species of *Lucina* Bruguiere necessitates the consideration of the valid name to be used for the *L jamaicensis* group Blainville's use of '*Phacoides*' was colloquial and adjectival (as was pointed out by Chavan (1937, **81**, no 2), who, nevertheless, used it) Agassiz's use of the name seems to be a *nomen nudum* as suggested by Neave (1939–40), since it is a mere quotation of Blainville's use of the word '*Phacoides*', in spite of Sherborn's interpretation that it refers to something different from the form referred to by Blainville The first valid use that I can find of the name *Phacoides* is that of H & A Adams, who use it in a proper generic sense as a synonym of *Lucina* Bruguière, giving *L jamaicensis* Spengler as an example of the genus The fact that the type species of *Lucina* Bruguière is not the species mentioned by H & A Adams as the example does not appear to mean that *Phacoides* must necessarily remain as a synonym of *Lucina* The only species mentioned by H & A Adams in the first valid use of the name becomes the type by monotypy This interpretation seems best, and has the added advantage of retaining a name that has been well known in the past as applying to the *L jamaicensis* group of shells The writer has shown elsewhere that the name *Anodontia* Link, which has been applied by Stewart (1930) to this group of shells, actually refers to those species previously referred to the genus *Loripinus* Monterosato

PHACOIDES PAKISTANICUS n sp

(Figures 75*a*, *b*, plate 13)

Material *Rakhi Nala section* Rubbly Limestones (local zone 6) (FB F 1910, *1*), Lower Chocolate Clays (local zone 10) (FB F 1966, the holotype, Reg No L 80067)

Description Shell of moderate size, transversely oval-suborbicular, moderately thick-shelled, rather flat, little inflated Umbos small, pointed, not prominent, gently prosogyrous, submedian Antero-dorsal margin of moderate length, almost straight, gently descendent Anterior end, ventral margin and posterior end convexly rounded, almost semicircular Posterior end vaguely truncated, sloping upwards slightly towards the umbos Postero-dorsal margin not very long, slightly convex, slightly descendent, meeting the posterior end high up in a very rounded and very obtuse angle Surface ornamented with fine, distinct, very widely spaced concentric threads, spaced about 2 mm apart in the adult portion of the shell There was apparently a relatively small anterior area, but this part of the shell is not well preserved Posterior area indistinct, only slightly excavated, separated off from the main portion of the surface of the shell along a line from the umbo to the postero-ventral corner Escutcheon a long, narrow, sunken area extending the whole length of the postero-dorsal margin

Dimensions Holotype length 15 3 mm , height 13 5 mm , thickness (both valves) 6 8 mm

Remarks *Lucina innesi* Cuvillier (1930, p 309, Pl 18, figs 21–23), from the Lutetian of Egypt, is a higher and more triangular species *L qurnaensis* Oppenheim as figured by Dareste de la Chavanne (1910*a*, Pl 1, figs 4–6), from the Eocene of Guelma (Algeria), is not so transverse The fine, widely spaced concentric threads and the transversely oval form appear to be characteristic

Genus *PSEUDOMILTHA* Fischer, 1887

(*Man Conch* p 1144)

Type species '*Lucina*' *gigantea* Lamarck, Eocene, monotypy

Remarks Chavan's (1937–38, **82**, no 2, p 106) view that *Pseudomiltha* should rank as a genus is adopted here

PSEUDOMILTHA GIGANTEA (Deshayes), 1825

References *Lucina gigantea* Deshayes, 1825 (p 91, Pl 15, figs 11, 12), Lamarck, 1835 (p 231), Bronn, 1848*a* (p 673), d'Orbigny, 1850 (p 385), d'Archiac & Haime, 1854 (pp 238, 241, 359, 365), Morris, 1854 (p 208), Pictet, 1855 (p 494), Lanza, 1856 (p 130), Lowry, 1866 (p 229), d'Archiac, in Tchihatcheff, 1866 (p 171), Fuchs, 1867 (p 194), K Mayer, 1869 (p 367), Fuchs, 1870 (p 142), Ball, 1874 (p 152), Vieillard & Dollfus, 1875 (p 100), Medlicott & Blanford, 1879*b* (p 459), Duncan, 1880 (p 9), Blanford, 1880 (p 48), Fedden, 1880 (p 201), Wynne, 1880 (p 84), Vasseur, 1882 (p 234), Cossmann 1883 (p 293), Zittel, 1883 (pp 93, 99, 103, 107), Romanowski, 1884 (p 102), Frauscher, 1886 (p 166), C Mayer-Eymar, 1887 (p 96), Newton, 1891 (p 44), Harris & Burrows, 1891 (p 17), Sokolow, 1893 (p 163), Oppenheim, 1894 (pp 444, 443), Oppenheim, 1896*a* (p 152), Vinassa de Regny, 1896*a* (pp 216, 212), Radkewitsch, 1900 (p 343), Oppenheim, 1901*b* (p 240), Oppenheim, 1903*a* (p 129), Fabiani, 1915 (pp 22, 144, 259, 277), Schlosser, 1922 (p 292), Oppenheim, 1923 (p 93), Abrard, 1925*a* (p 132), L M Davies, 1926*a* (p 367), Cuvillier, 1930 (p 34), Coulon, 1936 (pp 33, 34), Furon, 1941 (p 340)

Lucina indet , d'Archiac, 1850*b* (3, 261)

L (*Miltha*) *gigantea* Deshayes var *obliquopsis* de Gregorio, 1894*b* (p 35, Pl 7, figs 212, 213)

L gigantea Deshayes var *obliquopsis* de Gregorio, de Gregorio, 1896 (p 94, Pl 16, fig. 8?)

L gigantea Deshayes var *irradiata* de Gregorio, 1896 (p 94, Pl 16, figs 9, 10)

L (*Miltha*) *gigantea* Deshayes, Cossmann, 1887 (p 26), Harris & Burrows, 1891 (p. 71); de Gregorio, 1894*b* (p 35, Pl 7, fig 208), Dainelli, 1904 (pp 236, 154, 160), Checchia-Rispoli, 1912 (pp 93, 78), Oppenheim, 1923 (p 93)

Phacoides (*Pseudomiltha*) *giganteus* (Deshayes), Cossmann & Pissarro, 1904*a* (Pl 23, fig 82–1, Pl 25, fig 82–1), Cossmann, 1905 (p 148), Doncieux, 1911 (p 131), Furon & Soyer, 1947 (pp 94, 106)

P giganteus (Deshayes), Abrard, 1925*b* (pp 18, 31), Abrard, 1925*a* (pp 88, 89, etc), Robert, 1932 (p 25), Furon & Soyer, 1947 (Pl 12, fig 82–1)

Miltha gigantea (Deshayes), L & J Morellet, 1930 (p 467), L & J Morellet, 1948 (pp 29, 41, 77, 108, 114, 119, 124, 207)

Lucina (*Pseudomiltha*) *gigantea* Deshayes, Cox, 1931*a* (pp 75, 32, 34, 35, Pl 4, figs 4*a*,*b*)

Phacoides gigantea (Deshayes), Coulon, 1936 (p 37)

Pseudomiltha gigantea (Deshayes), Chavan, 1938 (**82**, no 2, p 107)

INCORRECT REFERENCES *Lucina* (*Miltha*) *gigantea* Deshayes, Kranz, 1910 (p 214)

Lucina gigantea Deshayes, Fabiani, 1915 (p 270)

MATERIAL *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 2) (FB F 1835, *3*, Reg No L 80068–70)

FURTHER DISTRIBUTION IN PAKISTAN ?Shekhan Limestone near Jutana, ?Laki of Sind, Khirthar of Sind, Eocene of Karundi, and the Luni Pathan Hills

FURTHER DISTRIBUTION The species has a long range and a wide geographical distribution The following summary will give a fair idea of the distribution and range Libyan of Egypt, Lutetian of France and Venetia, Middle Eocene of England, Switzerland, Dalmatia, Asia Minor, and Somaliland, Auversian of Venetia and Dalmatia, Barton Beds of Barton, Bartonian of France, Eocene of Traktomirow (Russia), Sicily, the northern Alps, Bolca, Monte Postale, and the Balkans

REMARKS Cox (1931*a*) has shown that de Gregorio's 1894*b* *Lucina* (*Miltha*) *gigantea* Deshayes var *subtruncata* and his *L* (*M*) *gigantea* Deshayes var *secunda* are to be omitted from the synonymy of the species, as are his 1896 records of *L gigantea* Deshayes var *secunda* and *L gigantea* Deshayes var *escheri* Mayer, and Fabiani's (1905) record of *L gigantea* Deshayes var *subtruncula* de Gregorio Kranz's (1910) and Fabiani's (1915) records of the species from the Oligocene of Vicentin and from the Middle Oligocene of Venetia are best disregarded, the records were unaccompanied by illustrations and probably refer to other species such as are known to the writer to occur in the Lower Nari of western Pakistan Blanford's (1880) and Fedden's (1880) records of the species from the Khirthar of Sind probably refer to occurrences subsequently placed in the Laki series by Cox Although the stratigraphical horizon of the Jutana occurrence was given as Shekhan Limestone, there is none in the area, the age is probably best regarded as Laki, although it is possible that it may be Sakesar Limestone

PSEUDOMILTHA NOORPOORENSIS (d'Archiac & Haime), 1854

REFERENCES *Lucina noorpoorensis* d'Archiac & Haime, 1854 (pp 241, 366), Cox, in L M Davies & Pinfold, 1937 (pp. 5, 7, 11), Krishnan, 1943 (p. 435)

L supragigantea de Gregorio, 1894*b* (p 36, Pl 8, figs 221, 222), Vinassa de Regny, 1896*a* (p 216), Vinassa de Regny, 1898 (p 168–?), Oppenheim, 1901*b* (p 164), Dainelli, 1915 (pp 78, 481), Fabiani, 1915 (2, 259)

L pullensis Oppenheim, 1894 (p 348 (pars), Pl 24, fig 1, *non* Pl 22, figs 4, 5), Oppenheim, 1896*a* (p 153 (pars)), Fabiani, 1915 (pp 33, 145), Oppenheim, 1917 (p 73)

L nokbaensis Oppenheim, 1903*a* (p 139, text-fig 10, Pl 10, fig 13), Cuvillier, 1930 (pp 94, 168), Stefanini, 1938 (p 29)

?*L immanis* Oppenheim, 1903*a* (p 140, Pl 15, fig 17), Desio, 1934 (pp 85, 92), Stefanini, 1938 (pp 25, 26, 29, 32, 34, 35, 43, 44, 47)

Lucina cf *menardi* Deshayes, Newton, 1905 (p 172, Pl 21, fig 8)

L pulliensis Oppenheim, Boussac, 1908 (p 242), Boussac, 1911*b* (pp 27 (pars), 36)

L (*Pseudomiltha*) *noorpoorensis* d'Archiac & Haime, Cox, 1931*a* (pp 76, 32, 34, Pl 4, fig 3)

L (*Miltha*) *supragigantea* de Gregorio, Szots, 1939 (p 180)

MATERIAL *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 2) (FB F 1841, *3*, Reg No L 80071–3)

FURTHER DISTRIBUTION IN PAKISTAN Dhak Pass Beds of the Salt Range, Khairabad Limestone of the Salt Range, Sakesar Limestone of the Salt Range, ?Upper Laki of Noorpoor (type locality), ?Laki between Warcha Mine and Sakesar Peak

FURTHER DISTRIBUTION Libyan of Egypt, Middle Eocene of Italy, Egypt, Hungary, Somaliland, south Arabia, Iraq, Persia and Asia Minor, Auversian of Italy and Biarritz, Eocene of numerous localities in Somaliland (Stefanini, 1938)

REMARKS Boussac (1911*b*) and Cox (1931*a*) have shown that only Pl 22, figs 4, 5 of Oppenheim's (1894) *Lucina pullensis*, which are from Monte Pulli, are to be taken as representative of the species, Pl 24, fig 1, which is from Monte Postale, being different, Fabiani's (1905, p 145) and Boussac's (1911*b*, p 27 (pars)) records of *L pullensis* and Cossmann's (1921*a*, p 94, Pl 5, figs 55–57) record refer to *Pseudomiltha pullensis* (Oppenheim)

PSEUDOMILTHA VREDENBURGI (Cossmann & Pissarro), 1927

REFERENCES *Phacoides* (*Pseudomiltha*) *vredenburgi* Cossmann & Pissarro, 1927 (p 30, Pl 4, figs 3–5, 36)

Lucina (*Pseudomiltha*) *vredenburgi* (Cossmann & Pissarro), Cox, 1931*a* (pp 77, 28, 34, Pl 4, fig 1)

L vredenburgi (Cossmann & Pissarro) Cox, in L M Davies & Pinfold, 1937 (pp 5, 7), Krishnan, 1943 (p 434)

MATERIAL *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2366, *2*, Reg No L 80199–80200, FB F 2367, *1*, Reg No L 80074), Middle Shekhan Limestone (local subzone 3*a*) (FB F 2370, *4*)

FURTHER DISTRIBUTION IN PAKISTAN Dhak Pass Beds of the Salt Range, Khairabad Limestone of the Salt Range, Upper Ranikot (zone 3), north of Leilan coal-pit, Upper Ranikot (zone 4) on road south-west of Jherruck, Shekhan Limestone of Kohat

Genus *ANODONTIA* Link, 1807

(*Beschr Nat Samml Univ Rostock*, pt 3, p 156)

Type species *Anodontia alba* Link, Recent = '*Venus*' *edentula* Linné, Dall, 1901, and monotypy

Synonyms *Loripinus* Monterosato, 1883 (*Natural Sicil* 3, 91), type species *Lucina fragilis* Philippi, Pliocene = *L edentula* Brocchi *non* Linné, Crosse, 1885

Eophysema Stewart, 1930 (*Spec Pub Acad nat Sci Philad* no 3, pp 37, 186), type species *Lucina subvexa* Conrad, Eocene, original designation

Remarks The writer has dealt fully with the identification of the genotype of *Anodontia* elsewhere (1951*a*)

ANODONTIA KOHATICA (Cox), 1931

References *Lucina* (*Loripinus*) *kohaticus* Cox, 1931*a* (pp 74, 28, 34, 35, Pl 4, figs 11*a*,*b*)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1897, *1*, Reg No L 80201)

Further distribution in Pakistan Laki of Sind, Kohat Shales of Harnai, Bahadur Khel and Kohat (type locality)

Remarks Although *Anodontia pharaonis* occurs abundantly in the Rakhi Nala section, only one specimen of *A kohatica* has been found The latter specimen agrees well with Cox's illustration, and the specific name is here retained At the same time, it is suggested that further collecting may show that the extremely elongate form of *A kohatica* falls within the limits of variation of *A pharaonis*, especially since it seems likely that the elongate form has been partly produced by crushing

ANODONTIA PHARAONIS (Bellardi), 1853

References *Corbis* sp d'Archiac, 1850*b* (3, 260)

Lucina pharaonis Bellardi, 1854 (p 190, Pl 2, fig 12), d'Archiac & Haime, 1854 (pp 354, 241, 366), Fedden, 1880 (p 202), Oppenheim, 1901*a* (p 319), Oppenheim, 1903*a* (p 124), von Klebelsberg, 1913 (pp 381, 376), Stefanini, 1921*a* (pp 106, 112, Pl 16(1), fig 4), Stefanini, 1921*b* (p 147), Blanckenhorn, 1921 (pp 86, 92, 93, 96, 99), Cuvillier, 1930 (pp 59, 85, 116, etc), Cox, in B S Thomas, 1931 (p 31), Cox, 1931*c* (p 235), Cox, in B Thomas, 1932 (p 364), Negri, 1934 (pp 240, 245), Desio, 1934 (pp 90, 85, Pl 6, fig 2), Stefanini, 1938 (pp 23, 26, 29, 32, 35, 43, 45, 47), Agnesotti, 1939 (pp 241, 240, Pl 19, figs 1*a*,*b*), Furon, 1941 (p 335), Rossi, 1942 (pp 171, 116, 118, 121, 125, 127, 131, 135, 139, 140, 142)

L bialata Bellardi, 1854 (p 191, Pl 2, fig 7)

L aegypthiaca Bellardi, 1854 (p 191, Pl 2, fig 8)

L cycloidea Bellardi, 1854 (p 192, Pl 3, fig 3)

L inflata Bellardi, 1854 (p 192, Pl 2, fig 11)

L vicaryi d'Archiac & Haime, 1854 (pp. 240, 365, Pl 17, figs 5, *a*), Fedden, 1880 (p. 202).

L subvicaryi d'Archiac & Haime, 1854 (pp 241, 237, 365, Pl 17, figs 6, *a*), Blanford, 1880 (p 127), Fedden, 1880 (p 202)

Corbis? *elliptica* d'Archiac & Haime, 1854 (pp 237, 365, Pl 16, figs. 13, *a*), Fedden, 1880 (p 201).

C? *subelliptica* d'Archiac & Haime, 1854 (pp 238, 359, 365, 354, Pl 16, figs 14, *a*), Fedden, 1880 (p. 201)

Lucina moevusi Coquand, 1862 (p 269, Pl 30, figs 17, 18)

L detrita Deshayes, Fraas, 1867 (p 142)

Corbis subelliptica d'Archiac, E Pavay, 1871 (p 366)

Lucina subvicaryi d'Archiac, Ball, 1874 (p 152)

L vicaryi d'Archiac, A von Pavay, 1874 (pp 364, 412), Mallada, 1890 (p 117), Mallada, 1892 (p 202)

Corbis elliptica d'Archiac & Haime, Blanford, 1880 (p 127)

Lucina pomum Dujardin, K Mayer-Eymar, 1883 (p 70, Pl 23, figs 19, ?20, 21)

L (?) *subvicaryi* d'Archiac & Haime, A Koch, 1894 (pp 264, 279, 297)

L libyca Cossmann, 1901 *b* (p 195(25), Pl 3, figs 16, 19)

L pharaonum Bellardi, Oppenheim, 1903 *a* (Pl 13, figs 1, 2, Pl 15, fig 6), Dareste de la Chavanne, 1910 *a* (pp 4, 40, Pl 1, figs 2*a*–*c*, Pl 5, fig 7), Blanckenhorn, 1921 (pp 88, 89), Flandrin, 1938 (p 144)

Diplodonta cycloidea (Bellardi), Oppenheim, 1903 *a* (p 147 (pars), Pl 13, figs 4, ?7, Pl 16, figs 1, 1*a*, 7, 7*a*, *non* Pl 13, figs 5, 6), Cuvillier, 1930 (pp 123, 168, 200, 204, 209, 215, 233, 270), Cuvillier, 1933 (p 13, Pl 2, fig 6), Negri, 1934 (p 245, Pl 5, fig 9), Desio, 1934 (pp 90, 85), Cuvillier, 1937 (p 231), Rossi, 1942 (pp 169, 116, 120)

D inflata (Bellardi), Oppenheim, 1903 *a* (p 149, Pl 16, figs 2, 3), Cuvillier, 1930 (pp 168, etc , 233, 270), Desio, 1934 (pp 90, 85, Pl 6, fig 1), Agnesotti, 1939 (pp 244, 239, 240, Pl 19, fig 4), Rossi, 1942 (pp 169, 116, 121, 131, 132)

Lucina (*Phacoides*) *pharaonum* Bellardi, Dareste de la Chavanne, 1910 *b* (p 149)

Lucina cf *pharaonis* Bellardi, Garde, 1911 (pp 92, 93, 95, 102), Pérébaskine, 1932 (pp 104, 47, 58, 60, 61, 62, 71, 117)

L pharaonis Bellardi form *transversa* von Klebelsberg, 1913 (p 381)

Corbis subelliptica(?) d'Archiac & Haime, A M Davies, 1923 (p 587 (pars))

Lucina (*Loripinus*) *pharaonis* Bellardi, Cox, 1931 *a* (pp 72, 28, 30, 33, 34, Pl 4, fig 8), Cotter, 1933 (p 98), Cox, 1936 (pp 32, 7, Pl 4, fig 2)

L pharaonis Bellardi var *bialata* Bellardi, Cuvillier, 1933 (p 14, Pl 3, figs 2–4), Rossi, 1942 (pp 17 (pars), 116, 128, 135)

L faronis Bellardi, Agnesotti, 1939 (pp 238, 239)

INCORRECT REFERENCES *Lucina pharaonis* Bellardi var *bialata* Bellardi, Desio, 1934 (pp 91, 85, Pl 8, fig 1)

MATERIAL *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1893, *10*+, FB F 1897, *4*, FB F 1899, *4*, FB F 1900, *10*+, FB F 1902, *4*, Reg No L 80202–5, FB F 1903, *10*+), Rubbly Limestones (local zone 6) (FB F 1904, *6*, FB F 1906, *1*, FB F 2051, *4*, FB F 1910, *10*+, FB F 1912, *10*+, FB F 1913, *4*, FB F 1914, *2*, FB F 1915, *1*, FB F 1916, *2*, FB F 1917, *6*, FB F 1918, *10*+), Shales with Alabaster (local zone 6) (FB F 1919, *6*), Shales with Alabaster (local zone 7) (FB F 1928, *4*, FB F 1929, *4*, FB F 1931, *10*+, FB F 1932, *10*+, FB F 1934, *10*+, FB F 1935, *10*+, FB. F 1938, *4*, FB F 1940, *1*, FB F 1943, *1*, FB F 1944, *6*, FB F 1945, *2*, FB F 1948, *6*, FB. F 1954, *6*), Lower Chocolate Clays (local zone 10) (FB F 1966, *6*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2558, *1*, FB F 2567, *2*, FB F 2732, *10+*, FB. F 2554, *10+*), White Marl Band (local zone 11) (FB F 2734, *10+*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *2*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *3*), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2292, *4*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *6*, FB F 2294, *15+*, FB F 2231, *1*, FB F 2232, *15+*, FB F 2287, *2*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *1*, FB F 2290, *2*, FB F 2291, *15+*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *15+*, FB F 2255, *3*, FB F 2295, *3*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *2*, FB F 2257, *2*), Nummulite Shales (local subzone 4*b*) (FB F 2266, *3*), Kohat Limestone (local subzone 4*b*) (FB F 2271, *3*), Kohat Limestone (local subzone 4*c*) (FB F 2275, *2*), *Kohat area* (*Shekhan Nala section*) Kaladhand Limestone (local subzone 4*a*) (FB F 2233, *7*, FB F 2334, *3*, FB F 2335, *15+*, FB F 2336, *7*), Upper Kohat Shales (local subzone 4*a*) (FB F 2337, *1*, FB F 2338, *1*, FB F 2342, *1*)

Accessory samples *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *4*, FB F 2184, *2*)

Further distribution in Pakistan Laki of Sind, Kohat Shales of Kohat, ?Khirthar of the Laki Valley, Khirthar of the Mari Hills, and the 'Alore Hills' (Sind), Eocene of the Luni Pathan Hills

Further distribution Ypresian of Algeria, Lower Eocene of eastern Sudan, Somaliland, Egypt and Tunis, Middle Eocene of Arabia, Sirtica, Libya, Egitto, Bahrein Island, Iraq, south Arabia and Egypt, Upper Mokattam of Egypt, Upper Eocene of the Balkans, Libya, Egitto and Sirtica, Eocene of Spain, Guelma, Tunis, the Soudan, Hungary, Arabia and numerous localities in Somaliland, Cyrenaica, Libya and Sirtica

Remarks Desio's 1934 record of *Lucina pharaonis* var *bialata* from the Eocene of Egypt is regarded as incorrect as the illustation shows a form with concentric ornament of the type found in *Pseudomiltha*, to which genus his specimens may belong *Lucina landanensis* E Vincent (1913, p 31, Pl 3, figs 12, 13, 14, 15), from the Palaeocene of the Belgian Congo, is more truncated posteriorly, and the impression of the anterior adductor muscle is more sinuous Blanford's records of the species from the Khirthar of the Laki Valley were made before the Laki Series was established, and might therefore be of Laki age

Records of *L pharaonis* Bellardi by Blanckenhorn, 1921 (p 112) and by Cuvillier, 1930 (pp 286, 287), and of *Lucina* cf *pharaonis* Bellardi by Cuvillier, 1930 (p 290) from the Oligocene of Egypt are here omitted None of the records is accompanied by illustrations, and it is considered that they probably refer to some other species such as are known to the writer to occur in the Lower Nari of western Pakistan

Family Fimbriidae

Genus *FIMBRIA*, M von Muhlfeld, 1811

(*Ges Nat Fr Berlin Mag* 5, pt 1, p 52)

Type species *Fimbria magna* M von Muhlfeld, Recent = *Venus fimbriata* Linné, monotypy

Synonyms *Venus* Linné, 1758 (pars)

Lucina Bruguière, 1797 (pars)

Gafrarium Roding, 1798 (pars)

Corbis Cuvier, 1817, type species *Venus fimbriata* Linné, monotypy

Idothea Schumacher, 1817 *non* Fabricius, 1798, type species *Idothea perforata* Schumacher, Recent = *Venus fimbriata* Linné, monotypy

REMARKS Nicol (1950) has drawn attention to the fact that the name *Fimbria* Bohadsch, 1761 is invalidated by Opinion 185 of the International Rules of Zoological Nomenclature

FIMBRIA LAMELLOSA (Lamarck), 1806

REFERENCES '*Chamae Chamitae*' Seba, 1765 (p 126, Pl 106, figs 59, 60)

'*Concha fossilis*, etc ' Chemnitz, 1782 (p 140, Pl 13, figs 137, 138)

Lucina Bruguière, 1797 (Pl 286, figs 2*a*,*b*)

L lamellosa Lamarck, 1806*a* (p 237), Lamarck, 1808 (Pl 42, figs 3*a*,*b*), Defrance, 1823 (p 276)

Corbis lamellosa (Lamarck), Lamarck, 1818 (p 537), Defrance, 1823 (p 270), Brongniart, 1823 (p 20), Bruguière, 1824 (p 154), Bronn, 1824 (p 51, Pl 5, fig 5), Deshayes, 1825 (p 88, Pl 14, figs 1–3), Deshayes, 1832*b* (p 6), Sturt, 1833 (p 254), Conrad, in Morton, 1834 (p 87 (pars)), Lamarck, 1835 (p 219), Galeotti, 1837 (p 158), Grateloup, 1838 (p 65), Anton, 1839 (p 6), Potiez & Michaud, 1844 (p 210), Nyst, 1845 (p 119), Geinitz, 1846 (p 438), Conrad, 1846 (p 36 (pars)), Bronn, 1848*a* (p 333), d'Archiac, 1850*b* (3, 259), d'Orbigny, 1850 (p 387), Bellardi, 1852 (pp 248, 294), Pictet, 1855 (p 489), d'Archiac, 1859*b* (p 788), Stache, 1862 (p 68), Hauer & Stache, 1863 (pp 262, 465), von Schauroth, 1865 (p 208), Vaillant, 1865 (p 281), d'Archiac, in Tchihatcheff, 1866 (p 168), Stache, 1867 (pp 263, 264), E Pavay, 1871 (pp 366, 424), Lartet, 1872 (p 72), A von Pavay, 1874 (p 412), Vieillard & Dollfus, 1875 (pp 66, 76, 100), Hébert & Munier-Chalmas, 1877 (p 263), Vasseur, 1882 (pp 228?, 234, 238, 257), Zittel, 1883 (p 82), Cossmann, 1887 (p 15), Harris & Burrows, 1891 (pp 17, 70), Cossmann, 1891*a* (p 26), Munier-Chalmas, 1891 (p 46), de Gregorio, 1894*b* (p 4), Oppenheim, 1894 (p 442), de Gregorio, 1896 (pp 94, 14, 17, 21, 22, 130), Oppenheim, 1896*a* (p 157), Vinassa de Regny, 1896*a* (pp 215, 236, 212, 227), Vinassa de Regny, 1897 (pp 159, 151), Radkewitsch, 1900 (p 341), Oppenheim, 1900*a* (p 21), Blanckenhorn, 1900 (pp 406, 417), Oppenheim, 1901*b* (p 184), Deninger, 1901 (pp 229, 240), Oppenheim, 1903*a* (p 152), Dainelli, 1904 (p 244, Pl 16(2), fig 1), Cossmann & Pissarro, 1904*a* (Pl 22, fig 78–1), Cossmann & Pissarro, 1904*b* (p 18, Pl 7, fig 8), Cossmann, 1905 (p 165, Pl 12, figs 1–3), Oppenheim, 1908 (pp 328, 316), Boussac, 1911*a* (p 216), Newton, 1911 (p 648, Pl 45, figs 12, 13), Fabiani, 1915 (pp 26, 30, 144, 259, 280, table opp p 178), Dainelli, 1915 (pp 482, 99, 117, 121, 129, 78, 412), Cossmann, 1921*a* (p 90, Pl 5, figs 41, 42), Blanckenhorn, 1921 (pp 82, 83, 87), Bourcart, 1922 (pp 69, 75, 76, 83), Abrard, 1925*b* (pp 18, 30), Abrard, 1925*a* (pp 44, 88, 89, 95, 96, 97, 98, 99, 102, 103, 104, 132, 133, 135, 148, 153, 173, 244, 266, 345, 348, 349, 350), Schlosser, 1925*b* (pp 21, 46), Goçev, 1926 (p 89), Cuvillier, 1930 (pp 118, 130, 169, 270), Robert, 1932 (p 25), Goçev, 1933*a* (pp 8, 73), Reina, 1933 (p 840), Reina, 1934 (pp 61, 7, 10, 13), Glibert, 1936 (pp 125, 207, Pl 4, fig 6), Coulon, 1936 (pp 32, 34), L & J Morellet, 1936 (p 296), Chavan & Dupuis, 1938 (p 534), Leriche, 1939*b* (pp B217, B255), Furon & Soyer, 1947 (pp 55, 94, 145, Pl 11, fig 78–1), L & J Morellet, 1948 (pp 28, 114, 119, 275, 281, 285, 330, 336, 342)

Corbis magna Anton, 1839 (p 6)

Fimbria lamellosa (Lamarck), Deshayes, 1858 (p 606), Fuchs, 1870 (p 142), G Vincent, 1873*b* (p 13), Fuchs, 1874 (p 134), Vincent & Rutot, 1879 (p 144), Vincent & Rutot, in Mourlon, 1881 (pp 189, 177), Nicolis, 1882 (p 94), Frauscher, 1886 (p 172(136)), C Mayer-Eymar, 1887 (p 97), Koch, 1894 (pp 264, 279), de Gregorio, 1894*b* (pp 34, 8), Timon-David, 1922 (p 90)

F davidsoni Deshayes, 1858 (p 607, Pl 48, figs 33–35)

Corbis cf *davidsoni* (Deshayes), Guembel, 1861 (p 652)

C davidsoni (Deshayes)?, d'Archiac, in Tchihatcheff, 1866 (p 167), Farchad, 1936 (pp 43, 23, Pl 1, figs 9*a*,*b*)

C boutillieri Cossmann, 1887 (p 19, Pl 1, figs 15, 16), Cossmann, 1891*a* (p 26)

Fimbria (*Corbis*) *lamellosa* (Lamarck), Mariani, 1892 (p 42), Koch, 1894 (p 286), Dainelli, 1915 (p 411), Timon-David, 1922 (p 94)

MATERIAL *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2377, *1*, Reg No L 80206)

FURTHER DISTRIBUTION *Fimbria lamellosa* has a long range in the Eocene and a wide geographical distribution, although it has not previously been recorded from India or Pakistan The following is a summary of its distribution Upper Libyan of the north Arabian Desert, Cuisian of the Paris Basin, Lower Eocene of the northern Alps, Bruxellian of Belgium, Lower Mokattam of Egypt, Middle Eocene of Italy, the Swiss Alps, France and Varna, Auversian of the Paris Basin and Italy, Bartonian of the Swiss Alps, Belgium, France and Albania, Upper Eocene of the Bavarian Alps, Upper Mokattam of Egypt, Eocene of Dalmatia, Istria, Hungary, Rumelia, Asia Minor, Bosnia, north-east Bulgaria, and south-west of Port Jackson (Australia), Palaeogene of the Isle of Rhodes, and Priabonian of Pomarole and Cyrenaica The records by Oppenheim (1908), from the Oligocene of the Bavarian Alps, were subsequently referred to the Upper Eocene, and Abrard's (1925*b*) record, from the Oligocene of Albania as well as from the Bartonian of Albania, seems very doubtful Later workers (e g Cossmann, and Oppenheim, 1896*a*) have shown that records of the species from the Eocene of New Holland, Clayborne and Alabama are incorrect Abrard's (1925*b*) inclusion of *Corbis distans* Conrad *sec* Cossmann (pars) (1893, *Ann Géol Paléont* **12**, 11) in synonymy is incorrect, as Cossmann did not include *C distans* in the synonymy of *C lamellosa*, and stated that '*C liratum* Conrad = *C distans* Conrad, and cannot be mistaken for *C lamellosa*' Newton's 1905 (p 172, Pl 21, fig 9) record of *Fimbria* cf *lamellosa* (Lamarck), from the Eocene of Somaliland, is of a fragmentary specimen which seems, however, to agree well with his 1911 record of the species from the Priabonian of Cyrenaica *Fimbria lamellosa* is smaller, less inflated, and with closer-spaced and more delicate radial ornament compared with *Corbis yuzgatensis* d'Archiac, in Tchihatcheff (1866, p 166, Pl 5, figs 4, *a*), from the Eocene of Asia Minor According to Schlosser 1922 (p 266), Dreger's 1903 (p 273) record of *C lamellosa* from Häring is probably to be referred to *Fimbria oligocaena* (Oppenheim)

Superfamily Tellinacea

Family Tellinidae

Genus *TELLINA* Linné, 1758

(*Syst Nat* 10th ed p 674)

Type species *Tellina radiata* Linné, Recent, Children, 1823

Synonyms *Musculus* Morch, 1853 *non* Bolten, 1798 (Moll) (*Cat Yoldi*, pt 2, p 13), type species quoted as *Tellina radiata* Linné, Recent

Liotellina Fischer, 1887 (*Man Conch* p 1147), type species *Tellina radiata* Linné, Recent, monotypy

TELLINA PAKISTANICA n sp

(Figures 76*a*,*b*, plate 13)

Material *Rakhi Nala section Venericardia* Shales (local zone 1) (FB F 1836, the holotype, Reg No L 80207)

Description Shell apparently very little inflated, transversely oval-subtriangular, narrower posteriorly Umbo small, pointed, not very prominent, submedian in position Antero-dorsal margin moderately long, almost straight in appearance, but really slightly convex, gently descendent Anterior end rather narrowly rounded Ventral margin gently to moderately convex Posterior end short, subvertical, slightly emarginate, situated slightly below the middle line, joining the postero-dorsal margin in a well-rounded and gentle curve, but joining the ventral margin in a sharply rounded obtuse angle, the ventral margin being straighter adjacent to this point than anteriorly Postero-dorsal margin moderately long, straight, gently descendent at about the same angle as the antero-dorsal margin A blunt ridge, with a vague depression behind it, runs from the umbo to the postero-ventral corner, separating off a posterior telliniform area Ornament consisting of numerous fine, closely spaced, concentric threads which are approximately of the same width as their intervals, and of which there are 5 in ¾ mm ventrally, in the earlier stages the threads appear flatter and with narrower, linear intervals

Dimensions Holotype length 26 1 mm , height 17 3 mm

Remarks The single specimen is an impression the form and ornament of which appear to be characteristic

TELLINA RAKHIENSIS n sp

(Figures 77*a*, *b*, plate 13)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1842, *1*, FB F 1844, *1*, FB F 1860, the holotype, Reg No L 80208), Green and Nodular Shales (local zone 4) (FB F 1867, *1*), Green and Nodular Shales (local zone 5) (FB F 1873, *1*)

Description Shell oval-subtriangular in outline, little inflated Umbos small, pointed, submedian Antero-dorsal margin of moderate length, gently convex, gently descendent Anterior end well rounded Ventral margin similarly well rounded, strongly convex Posterior end rather sharply rounded, situated fairly high up Postero-dorsal margin moderately long, practically straight, gently to moderately descendent. There is no posterior rostration Ornament consisting of extremely fine and narrow concentric threads with very wide intervals, the threads are 0 75 to 1 0 mm apart ventrally

Dimensions Holotype length 23 8 mm , height 19 2 mm

Remarks Although this species may not be a *Tellina* (*sensu stricto*), it is ornamented and apparently too short for a *Macoma* The subgenus *Arcopagiopsis* has much more distinct concentric ornament and the type species (*Tellina pustula* Deshayes) is distinctly smaller

Fig 16 of *Macoma yamadai* Nagao (1928, p 81(71), Pl 6, figs 3, 15, 16), from the Honso Beds of Japan (Namazuta fossil bed), is very similar in outline but apparently has fine radial ornament *Tellina haimei* Hebert & Renévier (1854, p 193, Pl 2, fig 2), from the Upper Nummulitic of Saint-Bonnet, is less orbicular and also apparently differs in the details of its ornament *Tellina* (*Moerella*) *patellaris* Lamarck as figured by Cossmann & Pissarro (1904*a*, 1, Pl 6, fig 35–24), from the Lutetian of Parnes, has more projecting and less forwardly placed umbos

Subgenus *PSAMMOTAEA* Lamarck, 1818

(*Syst An sans vert* **5**, 516)

Type species *Psammotaea donacina* Lamarck, Recent, Children, 1823

Synonyms *Donacilla* Gray, 1851 (*List Br Anim Br Mus* pt 7, p 39) *non* Lamarck, 1819, type species quoted as *Tellina donacina* Linné, Recent

Moera H & A Adams, 1856 (*Gen Rec Moll* **2**, 396) *non* Hubner, 1819 (Lepid), type species quoted as *Tellina distorta* Poli, Recent

Maera H & A Adams, 1856 (*Gen Rec Moll* **1**, Index to Gen p xxvii) (error)

Moerella Fischer, 1887 (*Man Conch* p 1147), type species *Tellina donacina* Linné, Recent, monotypy

Remarks There seems to be no reason why the name *Psammotaea* Lamarck, which is satisfactorily established, should not be used for those forms usually referred to *Moerella*

TELLINA (*PSAMMOTAEA*) *NANGGULANENSIS* Martin, 1915

References *Tellina* (*Moerella*) *nanggulanensis* Martin, 1915 (p 193, Pl 8, fig 218)

T nanggulanensis Martin, Cotter, 1923 (pp 11, 2, 3, Pl 3, figs 3, 4), Van der Vlerk, 1931 (p 286), Chhibber, 1934 (p 226), Cotter, 1938 (p 69)

Material Top of Eocene, immediately underlying the Upper Nari sandstones, of Domanda, Dera Ismail Khan district, North-West Frontier Province (1 well-preserved specimen, registered no L 77923) *Rakhi Nala section Pellatispira* Beds (local zone 15) (FB F 1981, 2 poorly preserved specimens, Reg No L 80210–1)

Further distribution Upper Eocene of Nanggulan, Java (type locality), Yaw Stage of numerous localities in Burma (see Cotter, 1923)

Remarks Although the Rakhi Nala specimens are not very well preserved they are obviously conspecific with the well-preserved specimen from Mr Pinfold's collection from Domanda, the Domanda occurrence is at approximately the same stratigraphical horizon as that from which the Rakhi Nala specimens were obtained The species appears to be common in and restricted to the uppermost Eocene of Burma, Java, and western Pakistan, and had not previously been recorded from the latter country

TELLINA (*PSAMMOTAEA*) *SUBDONACIALIS* d'Archiac & Haime, 1854

References *Tellina subdonacialis* d'Archiac & Haime, 1854 (pp 237, 240, 365, Pl 17, figs 1 bis, 1*a* bis), Boettger, 1877 (pp 54, 56), Cox, 1931*a* (pars) (pp 79, 34, 35)

Material *Rakhi Nala section* Rubbly Limestones (local zone 6) (FB F 1908, *1*, Reg No L 80212), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294, *2*)

Further distribution in Pakistan ? Laki of the 'Hala Range' (type locality)

Further distribution Upper Ypresian of Somaliland

Remarks All records of this species from the Miocene of India and Pakistan probably refer to an unpublished species which the writer, although not having seen the hinge or pallial sinus, believes to belong to the genus *Macoma* This form has been found in Miocene beds of several localities in western Pakistan and India, and has been recorded as the species *subdonacialis* from the Upper Gaj of the Maki Nai and the Khenji Nai, from the Gaj of Gaga and Bhogat, and from the Manchhar/Gaj Passage Beds of the Larkanda Nai Records of *Tellina* (*Macoma*) *subdonacialis* by Blanford, 1876 (p 16), of *T subdonacialis* by Medlicott & Blanford, 1879*b* (p 463), Duncan, 1880 (p 13), Blanford, 1880 (pp 54, 80, 89), Fedden, 1880 (p 201), Duncan & Sladen, 1885 (p 274), R D Oldham, 1893 (p 311), and Cox, 1931*a* (pars) (p 79), of *T sub-donacialis* by Fedden, 1884 (pp 49, 50), and of *T* (*Moerella*) *subdonacialis* by Vredenburg, 1928*b* (p 459), all refer to this Miocene form

Subgenus *EURYTELLINA* Fischer, 1887

(*Man Conch* p 1147)

Type species *Tellina punicea* Born, Recent, monotypy

TELLINA (*EURYTELLINA*) *GYPSIFERA* n sp

(Figures 78*a*, *b*, plate 13)

Material *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1938, *1*, FB F 1942, the holotype, Reg No L 80213, and 1 topotype, Reg No L 80214)

Description Shell transversely oval-subelliptical, flattened and very little inflated, the posterior end produced but slightly truncated Umbos small, pointed, submedian or very slightly anterior to the middle line Antero-dorsal margin long, almost straight, slightly convex, gently descendent Anterior end rather narrowly rounded Ventral margin horizontal as a whole, gently convex Posterior end vaguely truncated, more or less vertical, fairly straight, meeting the ventral and postero-dorsal margins in rounded, obtuse angles Postero-dorsal margin long, fairly straight, slightly descendent, sloping a little less steeply than the antero-dorsal margin Surface apparently smooth except for growth lines Posterior area not rostrate, but a little flattened compared with the upper portion of the anterior end

Dimensions Holotype length (broken) 25 6 mm , height 17 2 mm , thickness (both valves) 5 5 mm Dimensions according to a growth line are length 22 9 mm , height 11 8 mm

Remarks The specimens are moulds, but have a characteristic form *Tellina songoensis* Martin (1915, p 193, Pl 8, fig 219), from the Upper Eocene of Nanggulan, is larger, evidently has a distinct posterior keel, and is less transversely elliptical in outline *Tellina* (*Peronidia*?) sp of E Vincent (1913, p 32, Pl 3, fig 18), from the Palaeocene of the Belgian Congo, is a higher form

Genus *MACOMA* Leach, 1819

(*Ross*, *Voy* 2nd ed 2, 175)

Type species *Macoma tenera* Leach, Recent = *Tellina calcarea* Gmelin = *T lata* Gmelin *vide* Bucquoy, Dollfus & Dautzenberg, monotypy

Synonyms *Macroma* Gray, 1825 (*Ann Phil* **25**, 136) (*err typ*)

'*Psammotea* Turton' Gray, 1847, sec Dall, 1900 (*Proc Zool Soc Lond* p 186), type species' *Tellina solidula* Pultney, Recent, monotypy

Limicola Leach, in Gray, 1852 (*Syn Moll Gr Brit* p 296) *non* Koch, 1816 (Aves) *nec* Agassiz, 1846 (Aves), type species quoted as being *Tellina carnaria* Pennant, Recent

Macomopsis Sacco, 1901 (*I Moll terr terz Piem e Lig* **29**, 107), type species *Macomopsis elliptica* (Brocchi), ?Oligocene-Miocene-Pliocene, original designation

MACOMA SAFAEDENSIS n sp

(Figures 96*a*, *b*, *c*, 97 *a*, *b*, *c*, plate 15)

Material Lower Chocolate Clays east of Safaed, south of Tobah, Dera Ghazi Khan district, Punjab (the holotype, Reg No L 77888) *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1966, *1*, Reg No L 80215)

Description Shell transversely subelliptical-subtriangular, slightly cuneiform on account of a slightly concave antero-dorsal margin, only moderately inflated Umbos small, pointed, distinct, rather prominent, only very slightly prosogyrous, submedian in position Antero-dorsal margin long, gently descendent, slightly concave Anterior end narrowly rounded Ventral margin moderately convex, with a tendency to be more so in its anterior half, the posterior half being straighter and vaguely emarginate Posterior end rather narrow, produced, subvertical, gently convex, vaguely truncated, merging into the ventral margin in a rounded obtuse angle, and merging into the postero-dorsal margin more imperceptibly Postero-dorsal margin long, practically straight, a little more steeply descendent than the antero-dorsal margin Ornament consisting of sharp, distinct, widely spaced, concentric threads (of which there are 4 in ¾ mm ventrally) separated by rather wide intervals in which there are numerous very fine, microscopic growth lines Valve margins internally smooth Escutcheon a short, narrow, lanceolate hollow situated at the umbonal end of a large, long, lanceolate depression limited by a distinct ridge on each side, and distinctly steep-sided There is a similar large area anterior to the umbos, but it is less deep, less well limited, and becomes very ill-defined distally The Rakhi Nala specimen shows part of the impression of the pallial sinus which is widely sub-rhombic in shape, the apex being at about half the length of the shell or perhaps slightly more.

Dimensions Holotype length 32 1 mm , height 20 0 mm , thickness (both valves) 8 9 mm

Remarks *Tellina lorioli* C Mayer-Eymar (1887, p 41, Pl 3, fig 14), from the Eocene of Thun (Switzerland), is more pointed posteriorly The pallial sinus and general form appear to place the Pakistan species as a *Macoma* rather than a *Tellina*

MACOMA PANOBAENSIS n sp

(Figures 98*a*, *b*, plate 15)

Material *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, *7*, FB F 2173, *2*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *4*), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2292, *1*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294, the holotype, Reg No L 80216, and 13 topotypes, Reg No L 80217–22), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2291, *4*)

Accessory sample *Kohat area* (*Tarkhobi*) Middle Shekhan (local zone 3) (FB F 2180, *1*)

Description Shell of moderately large size, transversely oval-subtriangular in outline, gently inflated Umbos small, pointed, moderately prominent, submedian in position Antero-dorsal margin long, almost straight, appearing very slightly concave on some of the topotypes but not on the holotype, gently descendent Anterior end rounded Ventral margin gently convex Posterior end narrowly rounded, situated slightly below the middle line Postero-dorsal margin long, straight, moderately steeply descendent, more so than the antero-dorsal margin

Dimensions Holotype length 38 7 mm , height 26 9 mm , thickness (both valves) 12 0 mm

Remarks The specimens are all moulds, none of them showing any ornament Although in some cases bearing a close resemblance to *Macoma safaedensis*, this species is normally larger, and the height is proportionately greater, the postero-dorsal margin being more steeply descendent *Tellina praeplanata* C Mayer-Eymar (1887, p 43, Pl 5, fig 3), from the Bartonian of Niederhorn (Thun), has distinctly less prominent umbos, the antero-dorsal and postero-dorsal margins being less steeply descendent, and the form more transversely subelliptical The form figured by Loss (1940, p 49, Pl 4, fig 5) as *T praeplanata* Mayer-Eymar, from the Priabonian (Upper Eocene) of Cimome, is, however, higher than *Macoma panobaensis*, the postero-dorsal margin, in particular, being more steeply descendent and the posterior end more pointed The Italian species has fine concentric ornament, and is apparently different *Tellina tenuistria* Deshayes (1824, p 80, Pl 12, figs 5, 6) and its variety (1824, Pl 11, figs 9, 10), from the Eocene of Chaumont and Parnes, is somewhat similar in shape, but is not quite so high, is larger, and the variety has a postero-ventral sinuosity

MACOMA SORIENSIS n sp

(Figures 79*a*, *b*, plate 13)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2558, the holotype, Reg No L 80223, and 2 topotypes, Reg No L 80224–5, FB F 2556, *5*, Reg No L 80226–30, FB F 2555, *6*)

Description Shell of moderate size, little or gently inflated, oval-subtriangular in shape, a little wider than high, with small, pointed, not very prominent, submedian umbos

Antero-dorsal margin of moderate length, slightly convex, moderately descendent Anterior end rounded Ventral margin rather straight, slightly convex Posterior end not as high as the anterior end, vaguely truncated Postero-dorsal margin of moderate length and moderately descendent, but a little shorter and a little more steeply descendent than the antero-dorsal margin None of the specimens shows any trace of ornament

Dimensions Holotype length (slightly restored) 21 0 mm , height 15 6 mm , thickness (both valves) 7 2 mm

Remarks The specimens are all moulds *Macoma panobaensis* n sp is larger and more triangular in shape *M yamadai* Nagao (1928, p 81(71), Pl 6, figs 3, 15, 16), from the Palaeogene (Namazutu fossil bed, Honso Beds, Nogata Group) of Japan, is not so elongate, Nagao's figs 3 and 16 seem to be the typical form, and his fig 15 shows a smaller, more elongate specimen which is evidently atypical, but does not resemble the Zinda Pir species very closely *Tellina saratovensis* Archangelsky (1904, p 122, Pl 7, figs 10, 12), from the Palaeocene of the Volga region (Saratov), is more pointed posteriorly *T subidonea* Netschaew (1897, p 113, Pl 5, fig 23), from the Eocene of the Volga region, has less prominent umbos and the shell is less triangular in outline *T laverdana* Canestrelli (1908, p 74, Pl 1, fig 6), from the Oligocene of Laverda, which has been compared by Canestrelli with *T* (*Macaliopsis*) *elliptica* Brocchi, is not only more transverse but has a posterior keel and concentric ornament *T ovata* Sowerby as figured by Nyst (1843, Pl 5, fig 3), from the Tertiary of Belgium, is a little larger and more pointed posteriorly *T pseudodonacialis* d'Orbigny as figured by Roedel (1935, p 30, Pl 1, fig 11), from the Palaeocene of Frankfurt-on-Oder, and by Cossmann & Pissarro (1904*a*, Pl 5, fig 35–8), from the Thanetian of Noailles, has higher umbos and is more pointed posteriorly *T oosteri* Mayer-Eymar as figured by Boussac (1911*a*, p 228, Pl 6, figs 48, 49), from the Auversian of the Niederhorn, is rather larger and has more projecting umbos *T* (*Peronidia*) *ganensis* Cossmann in O'Gorman (1923, p 4, Pl 1, figs 14, 15), from the Cuisian of Gan, is less transverse and has less prominent umbos, is less equilateral, and also has fine concentric ornament and a posterior fold *T beyrichi* Deshayes (1857, p 340, Pl 26, figs 14–16), from the Lower Sands of Vregny and Cuise-la-Motte, is smaller and has a more convex ventral margin *T* (*Moerella*) *donacialis* Lamarck as figured by Cossmann & Pissarro (1904*a*, Pl 6, fig 35–18), from the Lutetian of Mouchy and from the Bartonian, is less elongate and usually more strictly equilateral *T* (*Macaliopsis*) *hybrida* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 6, fig 35–33), from the Cuisian of Cuise, is probably a little less inflated and more elongate, and is ornamented

MACOMA OVATITRIANGULARIS n sp

(Figures 80*a*, *b*, plate 13)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2570, *2*, FB F 2556, the holotype, Reg No L 80231, and 5 topotypes, Reg No L 80232–6, FB F 2731, *1*)

Description Shell oval-triagular in outline, moderately well inflated when not crushed and flattened, with no trace of having had any ornament apart from growth lines Umbos small, pointed, not very prominent, submedian in position Antero-dorsal margin of moderate length, slightly convex, moderately descendent Anterior end well rounded Ventral margin distinctly convex, less so posteriorly Posterior end more narrowly rounded than the anterior end Postero-dorsal margin of moderate length, practically straight, a little longer and more steeply descendent than the antero-dorsal margin

Dimensions Holotype length 27 7 mm , height 22 1 mm , thickness (both valves) 13 3 mm

Remarks The specimens are all moulds *Tellina* (*Macaliopsis*) *speciosa* Edwards as figured by Glibert (1933, p 182, Pl 11, fig 9), from the Bruxellian of Neder-Ockerzeel (Belgium), is somewhat similar, but is a little larger, the umbos are a little higher, and the posterior end is more narrowly rounded *T nystii* Deshayes (1857, p 336, Pl 25, figs 5, 6), from the Upper Sands of Jeures, Etrechy and Morigny in France, from near Cassel and Weinheim in Germany, and from Delémont in Switzerland, and also figured by Wolff (1897, p 254, Pl 23, figs 11, 12), from the Oligocene of southern Bavaria, is more elongate and pointed posteriorly, and also has a posterior fold *T explanata* von Koenen (1894, p 1266, Pl 88, figs 4, 5), from the Lower Oligocene of Lattorf, is a little larger, somewhat more pointed posteriorly and more transverse in its outline *T* (*Moerella*) *calcifera* Dufour as figured by Vasseur (1917, Pl 12, figs 27–32), from the Eocene of Bois-Gouet, and as figured by Cossmann (1906, p 223, Pl 17, figs 11–13), is less inflated, has higher umbos, and is more triangular in outline *Arcopagia namnetensis* Cossmann, in Vasseur (1917, Pl 12, figs 33–35), from the Eocene of Bois-Gouet—see also Cossmann (1906, p 220, Pl 17, figs 4–6)—superficially resembles *Macoma ovatitriangularis*, but is less inflated, not smooth, the umbos are a little higher, and the posterior end is more acutely pointed but less produced, *Tellina pseudo-donacialis* d'Orbigny as figured by Deshayes (1857, p 334, Pl 27, figs 1, 2) from the Lower Sands of Noailles, is more elongate, Cossmann & Pissarro's illustration (1904*a*, Pl 5, fig 35–38) of *T* (*Peronidia*) *pseudodonacialis* d'Orbigny, from the Thanetian of Noailles, Albercourt, and Vaux-sous-Laon, also has a straighter postero-dorsal margin *T* (*Moerella*) *donacialis* Lamarck as figured by Cossmann & Pissarro (1904*a*, Pl 6, fig 35–18), from the Lutetian of Mouchy and from the Bartonian, is less inflated, not so high, and relatively longer anteriorly

Genus *APOLYMETIS* Salisbury, 1929

(*Proc Malac Soc Lond* 18, 258)

Type species '*Tellina meyeri* Philippi', Recent = *T meyeri* Dunker, *vide* Philippi, monotypy

Synonyms *Capsa* Bruguière (1791) 1797 (pars) *auct*

Capsa Lamarck, 1799 *non* Bruguière 1797

Metis H & A Adams, 1856 (*Gen Rec Moll* 2, 399) *non* 1857 *nec* Philippi, 1843 (Crust) *nec* Gistl, 1848 (Echin), type species *Tellina meyeri* Philippi, Recent, monotypy.

'*Lutricola* Blainville', Carpenter, 1863 (*Sup Rep Brit. Ass* p 639) *non* Blainville, 1825, type species quoted as *Lutricola alba* Carpenter, Recent

Polymetis Salisbury, 1929 (*Proc Malac. Soc. Lond* 18, 255) *non* Walsingham, 1903 (Insecta), type species *Tellina meyeri* Dunker, Recent, original designation

APOLYMETIS TARKHOBIENSIS n sp

(Figures 99*a*, *b*, plate 15)

MATERIAL *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, the holotype, Reg No L 80237, and 2 topotypes, Reg No L 80238–9)

DESCRIPTION Shell of moderately small size, transversely suboval, tending to cuneiform, moderately strongly inflated Posterior fold on left valve not well preserved on any of the specimens, that on the right valve subvertical, sloping downwards slightly away from the middle line, fairly straight, slightly convex towards the posterior side, not forming any marked angulation of the ventral margin although the outline behind it is slightly emarginate Umbos small, pointed, not markedly prominent, situated posterior to the middle line at about one-third of the length Antero-dorsal margin moderately long, slightly concave on the holotype, straighter on some other specimens, slightly to gently descendent Anterior end rounded Ventral margin gently convex, straighter in its posterior portion Posterior end forming a bluntly rounded angulation at about half the height of the shell, the adjacent margins being fairly straight and forming similar angles with the vertical Postero-dorsal margin relatively short, slightly convex, rather steeply descendent Posterior fold distinct, surface of shell somewhat depressed adjacent to it, the anterior half of the shell being the more strongly inflated There is very little angulation at the postero-ventral corner, the ventral margin receding upwards regularly in a posterior direction to the posterior end Ornament not preserved

DIMENSIONS Holotype length 18 2 mm , height 13 7 mm , thickness (both valves) 7 8 mm

REMARKS The specimens are all moulds *Tellina* (*Arcopagia*) *tazuvensis* Cotter (1923, p 12, Pl 3, figs 5, 6), from the Yaw Stage of Burma and from the Upper Eocene of Java (see Martin, 1931, p 48, Pl 7, figs 7, 8)—which is an *Apolymetis*—is much larger, has less posteriorly placed umbos, a more sinuous ventral margin, and is distinctly higher anteriorly *A tarkhobiensis* somewhat resembles *Abra turgidula* Cossmann (1922*b*, p 132, Pl 4, figs 16, 17), from the Eocene of Bois-Gouët, but is larger, usually a little longer and more cuneiform, the posterior fold sharper and more vertical, and the ventral margin more regularly curved

APOLYMETIS KOHATICA n sp

(Figures 100*a*, *b*, 101, plate 15)

MATERIAL *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2377, the holotype, Reg No L 80240, and 4 topotypes, Reg No L 80241–4)

DESCRIPTION Shell of large size, rather strongly inflated, oval-subtriangular in outline Umbos high, projecting, prominent, small-tipped, slightly prosogyrous, situated at about two-fifths of the length Antero-dorsal margin moderately long, slightly convex, gently descendent Anterior end well rounded Ventral margin gently to moderately convex Posterior end forming a blunt angulation situated at about half the height of the shell Postero-dorsal margin of moderate length, a little shorter than the antero-dorsal margin, practically straight, rather steeply descendent Posterior fold very steeply descendent, nearly vertical, sloping downwards a little towards the posterior end, slightly convex towards the posterior end Surface apparently ornamented with distinct concentric threads and growth lines There is a little variation in the shape, some specimens being less elongate than the holotype

Dimensions Holotype length 57 6 mm , height 44 2 mm , thickness (both valves) 26 0 mm

Remarks The specimens are all moulds, although some of them retain traces of the concentric ornament which was present *Tellina* (*Arcopagia*) *tazuvensis* Cotter (1923, p 12, Pl 3, figs 5, 6), from the Yaw Stage of Burma (see also Martin, 1931, p 48, Pl 7, figs 7, 8, who records it from the Upper Eocene of Java), is somewhat smaller, has less prominent umbos, is less inflated, and higher anteriorly, and has less conspicuous ornament *Metis olssoni* Caster (1938, p 71, Pl 4, figs 6–9), from the Eocene of Angola, is smaller and has less vertical posterior folds *Tellina granconensis* Oppenheim (1901 *a*, p 170, fig 17), from the Priabonian of Grancona, is smaller, less produced anteriorly, and has less vertical posterior folds *T sinuata* Lamarck as figured by Deshayes (1824, p 79, Pl 11, figs 15, 16), from the Eocene of Grignon and Mouchy, is distinctly smaller and usually less elongate

Family SCROBICULARIIDAE

Genus *ABRA* Leach, in Lamarck, 1818

(*Hist nat An sans Vert* **5**, 492)

Type species *Mactra tenuis* Montagu, Recent, monotypy

Synonyms *Syndosmya* Recluz, 1843 (*Rev Zool* (*Soc Cuv*), **6**, 359), type species if not selected, to be chosen from the following nine Recent species *S alba* (Wood), *S tenuis* (Montagu), *S truncata* (Brown), *S purpurascens* (Lamarck), *S nucleola* (Lamarck), *S occitanica* Recluz, *S segmentum* (Costa), *S prismatica* (Laskey) and *S apelina* (Renieri)

Syndesmya, *em auct*

Syndesmia L Agassiz, 1846 (*em*) (*Nomen Zool Index Univ*)

Orixa Leach, in Gray, 1852 (*Syn Moll Gt Brit* pp 277, 280), type species *O tenuis* (Montagu), Recent, monotypy

Dorvillea Leach, in Gray, 1852 (*Syn Moll Gt Brit* pp 283, 286), type species *D anglica* Leach, in Gray, Recent, monotypy

Lutricularia Monterosato, 1884 (*Nomencl Conch medit* p 28), type species if not selected, to be chosen from the following two Recent species *L ovata* (Philippi) (=*Amphidesma segmentum* (O G Costa)=*Syndosmya caillaudi* Fischer=*Scrobicularia fabula* Brusina) and *Lutricularia tenuis* (Montagu)

Lutricolaria Cossmann & Peyrot, 1909 (error) (*Actes Soc Linn Bordeaux*, **63**, Fasc 4, p 287)

ABRA PAKISTANICA n sp

(Figures 102*a*, *b*, plate 15)

Material *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 13) (FB F 2520, *1*, FB F 2519, the holotype, Reg No L 80245, and 1 topotype, Reg No L 80246)

DESCRIPTION Shell of moderate size, moderately thin-shelled, smooth except for growth lines, oval-subtriangular in outline, moderately strongly inflated Umbos small, not very prominent, apparently slightly opisthogyrous, situated slightly posterior to the middle line at about two-fifths to nine-twentieths of the length Antero-dorsal margin of moderate length, practically straight, very slightly convex, gently descendent Anterior end rounded Ventral margin moderately convex Posterior end fairly regularly rounded Postero-dorsal margin moderately short, slightly convex, moderately steeply descendent No lunule No escutcheon, the ligament being apparently internal

DIMENSIONS Holotype length 18 8 mm , height 14 9 mm , thickness (both valves) 8 9 mm

REMARKS Although superficially resembling *Tellina* (*Psammotaea*) *nanggulanensis* Martin, it is not flexuous posteriorly, the umbos are more projecting, the shell is more inflated, and there is no external ligament *Abra deshayesi* (Bosquet) as figured by Glibert (1936, p 157, fig 65), from the Wemmel Sands of Jette (Belgium), and by Cossmann & Pissarro (1904*a*, Pl 5, fig 31–9), from the Bartonian of La Guépelle, is smaller and more pointed posteriorly, and has some indication of a posterior fold *Tellina* (*Moerella*) *donacialis* Lamarck as figured by Cossmann (1921*a*, p 37, Pl 2, figs 25–27), from the Auversian of Pédelay (Aquitaine), and by Cossmann & Pissarro (1904*a*, Pl 6, fig 35–18), from the Lutetian of Mouchy and from the Bartonian, is smaller, less inflated, and a little more elongate *Abra suessoniensis* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 5, fig 31–3), from the Cuisian of Cuise, is smaller and more transverse

Family GARIDAE

Genus *MACROSOLEN* Mayer-Eymar, 1883

(*Palaeontographica*, **30**, 116)

TYPE SPECIES *Sanguinolaria* (*Macrosolen*) *hollowaysii* J Sowerby, Middle Eocene, monotypy

SYNONYM *Latosiliqua* de Gregorio, 1894 (*Ann Géol Paléont* **13**, 18), type species *Solen* (*Latosiliqua*) *plicatus* von Schauroth, Eocene, original designation

MACROSOLEN(?) *CYCLOPEUS* (Brongniart), 1823

REFERENCES *Cypricardia cyclopea* Brongniart, 1823 (pars) (p 82, Pl 5, fig 12*a*—*non* figs 12*b*,*c*), Bronn, 1831 (p 105), Bayan, 1870 (p 456), Oppenheim, 1894 (p 442), de Gregorio, 1896 (p 98, Pl 18, figs 9–13), Vinassa de Regny, 1897 (p 160)

Solecurtus cyclopeus (Brongniart), d'Orbigny, 1850 (p 321)

Trapezium cyclopeum (Brongniart), Cox, 1931*a* (pp 71, 27, 28, 34, 35, Pl 3, figs 17, 18)

MATERIAL *Rakhi Nala section Pellatispira* Beds (local zone 15) (FB F 1980, *1*, Reg No L 80247), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *7*)

FURTHER DISTRIBUTION IN PAKISTAN Ghazij Shales of Hindu Bagh

FURTHER DISTRIBUTION Auversian or Middle Eocene of Ronca (near Verona) (type locality)

Remarks A feature of the forms from Pakistan, which is not indicated in Cox's illustrations and which is not preserved in the Rakhi Nala specimen recorded here, is the presence of two faint, but distinct, moderately closely spaced radial folds extending from the umbos slightly backwards to the ventral margin This feature is similar to that observed in *Azorinus* and *Macrosolen*, and is a character which excludes the species from the genus *Trapezium* Neither Brongniart's nor de Gregorio's illustrations indicate these folds Brongniart may have overlooked them, as they are not strongly marked, and de Gregorio's illustrations are of moulds which do not always have them preserved On the assumption that the Pakistan specimens are conspecific with the Italian form as suggested by Cox, which seems reasonable, the writer refers the species provisionally to the genus *Macrosolen*, since in its general form it resembles this genus more closely than *Azorinus* The Rakhi Nala specimen shows the presence of some fine concentric threads spaced 0 75 to 1 0 mm apart ventrally

MACROSOLEN PAKISTANICUS n sp

(Figures 103*a*, *b*, plate 15)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1967, the holotype, Reg No L 80248)

Description Shell large, not very thick-shelled for its size although the hinge plate is rather massive, transversely subelliptical, narrow and produced anteriorly, truncated posteriorly, moderately inflated, the greatest inflation being in the umbonal region Umbos small, broad, prosogyrous, not prominent, situated anterior to the middle line at about three-sevenths of the length Antero-dorsal margin long, straight to slightly convex, very slightly descendent Anterior end narrowly rounded Ventral margin long, subhorizontal, slightly convex anteriorly where it merges into the anterior end, straight medially and posteriorly Posterior end moderately convex, subvertical in its lower portion where it meets the ventral margin in a rounded angulation, moderately convex in its upper portion where it sweeps round and upwards towards the postero-dorsal margin Postero-dorsal margin rather long, very straight, and horizontal Ornament consisting of rather coarse, *Clementia*-like folds in the early stages (about 2½ mm apart and a little wider than their intervals) which fade out into irregular, accentuated growth lines on the middle and adult portions of the surface Two distinct folds radiate from the umbos, the posterior one travelling to the postero-ventral corner, the anterior one to a position a little way anterior to it on the ventral margin These folds slope downwards in a posterior direction from the umbos, are slightly convex on their postero-dorsal side in the early stages, but become straighter later, they are not very broad, and are separated by an interval about three or four times as wide as themselves Valve margins internally smooth Nymph prominent, of moderate length

Dimensions Holotype length (incomplete) 80 7 mm , height 48 3 mm , thickness (both valves) 25 6 mm Relative dimensions measured along one of the growth lines are length 56 3 mm , height 25 7 mm

Remarks The single specimen is broken posteriorly but otherwise well preserved The species is relatively higher and shorter posteriorly than *Solecurtus zwierzyckii* Martin (1931, p 45, Pl 6, fig 16), from the Upper Eocene of Nanggulan in Java The form and ornament of the Rakhi Nala species appear to be characteristic

MACROSOLEN PSEUDOANNULIFERUS n sp

(Figure 104, plate 15)

Material *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 14) (FB F 2517, the holotype, Reg No L 80249)

Description Shell transversely elongate-elliptical in outline Umbos small, rather broad, not prominent, prosogyrous, situated well anterior to the middle line Antero-dorsal margin relatively not very long, apparently slightly convex and slightly to gently descendent Anterior end broken, but the growth lines show that it was narrowly rounded Ventral margin very long, straight, subhorizontal Posterior end moderately convex, evidently somewhat angulated at its junction with the ventral margin, sweeping upwards towards the postero-dorsal margin with a more pronounced curvature than in its lower portion Postero-dorsal margin very long, slightly convex, subhorizontal near the umbos, becoming gently descendent distally The shell has been somewhat crushed, but it is evident that the umbonal region was moderately well inflated compared with the ventral region which was less inflated Two distinct folds radiate from the umbos, the posterior one going to the postero-ventral corner, the anterior one a little anterior to it, they are fairly straight and separated by an interval approximately three times as wide as they are Surface of shell posterior to the anterior radial fold ornamented solely with fine growth lines, that portion of the surface anterior to the anterior radial fold, however, is ornamented with strong, distinct concentric folds of about the same width as their intervals and spaced about 2½ to 3 mm apart ventrally

Dimensions Holotype length 56 9 mm (somewhat incomplete anteriorly), height 23 4 mm , thickness (both valves, but somewhat crushed) 18 1 mm

Remarks The only species bearing any close resemblance to this form is *Siliqua annulifera* Boettger (1875, p 26, Pl 4, figs 33*a*,*b*), from stage *β* of the Eocene of Borneo, which is, however, more cuneiform, has the radial folds apparently more distinctly curved, and, in particular, has coarse concentric folds all over the surface

Superfamily Chamacea

Family Chamidae

Genus *CHAMA* Linné, 1758

(*Syst Nat* 10th ed p 691)

Type species *Chama lazarus* Linné, Recent, Children, 1823

Synonyms *Jataronus* (Adanson, 1757) Bruguière, 1792 (*Encycl Meth* (*Vers I*), p 546) (name without species)

Maceris Modeer, 1793 (*K svenska VetenskAkad Nya Handl* **14**, 174) (name without species)

Psilopus Poli, 1795 (*Test Sicil* **2**, 112) (not binomial)

Psilopoderma Poli, 1795 (*Test Sicil* **2**, 253, 258) (not binomial)

Globus (Klein, 1753) Deshayes, 1832 (*Encycl Meth* (*Vers*), **2**, pt 2, p 170) *non* Scopoli, 1772 (Verm) (name without species)

Lacinea (Humphrey, 1797) Sowerby, 1842 (*Conch Man*, 2nd ed p 168) (=*Chama*)

Macerophyllum (Meuschen, 1766) Herrmannsen, 1847 (*Indicis Gen Malac* **2**, 1) (=*Chama*)

Psiloderma Fischer, 1887 (*Man Conch* p 1048) (*err pro Psilopoderma*)

CHAMA BRIMONTI d'Archiac & Haime, 1854

References *Chama calcarata* Lamarck, d'Archiac, 1850*b* (**3**, 267 (pars), 198)

Chama brimonti d'Archiac & Haime, 1854 (pp 267, 359, 367, Pl 23, fig 8), Fedden, 1880 (p 204), Cox, 1931*a* (pp 84, 34, 35)

Chama geslini d'Archiac & Haime, 1854 (pp 267, 359, 367, Pl 23, fig 8) Fedden, 1880 (p 204), Brown, 1931 (p 267)

Incorrect reference *Chama geslini* d'Archiac, A von Pavay, 1874 (p 413)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1843, *2*), Green and Nodular Shales (local zone 6) (FB F 1893, *1*, FB F 1897, *2*, FB F 1898, *2*, FB F 1899, *6*, FB F 1900, *1*, FB F 1901, *1*, FB F 1902, *2*, FB F 1903, *9*, Reg No L 80250–5), Rubbly Limestones (local zone 6) (FB F 1906, *4*, FB F 1908, *2*, FB F 1910, *1*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2571, *6*), *Kohat area* (*Tarkhobi section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2166, *1*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, *15*+, FB F 2172, *1*, FB F 2173, *15*+), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *15*+), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2223, *1*, FB F 2293, *2*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *15*+, FB F 2294, *15*+, FB F 2287, *5*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *15*+, FB F 2290, *9*, FB F 2291, *15*+), *Kohat area* (*Shekhan Nala section*) Kaladhand Limestone (local subzone 4*a*) (FB F 2336, *2*), Upper Kohat Shales (local subzone 4*a*) (FB F 2339, *1*, FB F 2341, *15*+, FB F 2342, *15*+), Nummulite Shales (local subzone 4*b*) (FB F 2346, *1*), *Kohat area* (*Gada Khel*) Middle Shekhan (local zone 3) (FB F 2104, *1*)

Further distribution in Pakistan Meting Limestone of Sind, Laki of Sind

Further distribution Middle Eocene of Somaliland

Remarks Specimens from the Laki Series all seem to belong to one species, and the writer sees no reason for regarding *Chama geslini* as a separate species, Cox (1931*a*) suspected that the two forms were conspecific A von Pavay's record of the species from the Middle Eocene of Hungary has never been substantiated, and can be disregarded Cox recorded that he found no radial ornament on the Pakistan species, but some of the specimens here recorded do show it The radial ornament is more closely spaced than in *C calcarata* Lamarck with which the species has been compared Apart from the difference in the nature of the spines, which has been described by Cox, the Pakistan species is normally a higher and less orbicular one than *C calcarata*, and moulds often show a ventrally produced ventral margin and shouldered lateral outline, producing a general sub-rhombic appearance

Superfamily Cardiacea

Family Cardiidae

Genus *PLAGIOCARDIUM* Cossmann, 1886

(*Ann Soc Malac Belg* **21**, 168)

Type species *Cardium granulosum* Lamarck, Eocene, Sacco, 1889

Subgenus *SCHEDOCARDIA* Stewart, 1930

(*Spec Publ Acad Nat Sci Philad* no 3, pp 38, 255)

Type species *Cardium hatchetigbeense* Aldrich, Eocene, original designation

PLAGIOCARDIUM (*SCHEDOCARDIA*) *SPARSISPINOSUM* n sp

(Figures 105*a*, *b*, *c*, *d*, plate 15)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1967, the holotype, Reg No L 80256)

Description Shell small, suboval in outline, a little wider than high, moderately strongly inflated Umbos rather small, not very prominent, prosogyrous, situated anterior to the middle line at about two-fifths of the length Anterior, ventral, and posterior margins well rounded, the posterior end being slightly the higher, the ventral margin the least convex Ornament consisting of about 23 radial ribs of very characteristic appearance These ribs are square in section and of the same width as their intervals, well raised on account of the depth of the intervals, each one carrying a coarse longitudinal thread which is not quite as wide as the rib and which is marked off from the rib by a pair of undercutting grooves, these coarse threads in turn carry wide-spaced ventrally projecting, hollow spines which rise up gradually in a ventral direction and end with an abrupt vertical face The spines are spaced about 1 7 mm apart in the adult shell Intervals carrying fine, closely spaced, slightly raised concentric threads which are somewhat convex on their ventral side, and about 8 in ¾ mm in number

Dimensions Holotype length 10 4 mm , height 9 6 mm , thickness (both valves) 7 5 mm

Remarks Although the hinge is not seen, and although the shell is less trapezoidal in outline and the umbos not so large as in *Cardium hatchetigbeense* Aldrich from the Eocene of Alabama (the type species of *Schedocardia*), the Pakistan species is referred to the subgenus *Schedocardia* on account of the nature of the ornament (evidently an important criterion in the classification of the members of the Cardiidae), and of the fact that it is a little wider than high Stewart (1930) states that 'the name *Schedocardia* is probably better used only for the American species and possibly species from the Burman and Japanese Eocene mentioned under *P brewerii*' The Japanese species is *Cardium mukense* Nagao, and the Burmese species is *C thetkegyinense* Cotter As far as the Burmese species is concerned, there are never any spines present, even on well-preserved specimens, and the species appears more likely to be a *Trachycardium* The presence of the subgenus *Schedocardia* in the Eocene of Western Pakistan is, however, by no means surprising

Cardium (*Plagiocardium*?) *charcovensis* Slodkewitsch (1928, p 557, Pl 38, figs 3*a*,*b*,*c*), from the Palaeogene of the Donetz basin, has distinctly higher umbos, is less regularly transversely oval, has more numerous ribs which are blunter and have much less distinct intervals, and has less widely spaced spines on the ribs

Genus *TRACHYCARDIUM* Morch, 1853

(*Cat Yoldi*, **2**, p 34)

Type species *Cardium isocardia* Linné, Recent, von Martens, 1869

Synonym *Granocardium* Gabb, 1868 (*Geol Surv Calif*, *Pal* **2**, 266), type species *Cardium carolinum* d'Orbigny, Cretaceous, Stewart, 1930

Remarks As a result of recent research, the following Eocene species placed in the genus *Trachycardium* may be found to belong to a distinct subgenus

TRACHYCARDIUM HALAENSE (d'Archiac & Haime), 1854

References *Cardium subasperulum* d'Archiac, 1850*b* (**3**, 264, *nomen nudum*) *non* d'Orbigny, 1850

C halaense d'Archiac & Haime, 1854 (pars) (pp 257, 367, Pl 21, figs 19, *a*,*b*, 20), Blanford, 1880 (p 127), Fedden, 1880 (p 203), ?Oppenheim, 1903*a* (p 154, Pl 11, fig 14, *non* fig 13), Garde, 1911 (p 99), Cossmann & Pissarro, 1927 (pp 22, 4), Cox, 1930*a* (p 205), Cox, 1931*a* (pp 83, 28, 34), Cotter, 1933 (p 98), Negri, 1934 (pp 248, 252)

?*C austeni* d'Archiac & Haime, 1854 (pp 257, 367, Pl 21, figs 18, *a*,*b*) *non* Forbes, 1845, Fedden, 1880 (p 203)

C halaense d'Archiac, Boettger, 1877 (pp 72, 73), Netschaew, 1897 (p 245), Cuvillier, 1930 (pp 57, 59, 85, 105, 169, 216, 271)

?*Cardium* cf *halaense* d'Archiac & Haime, Oppenheim 1915 (p 24, Pl 1, fig xvi)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2556, *3*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *9*, Reg No L 80257–62), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *6*), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2292, *2*, FB F 2293, *2*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *2*, FB F 2294, *10*, FB F 2287, *7*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *1*, FB F 2291, *15*+), *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2377, *1*), Upper Kohat Shales (local subzone 4*a*) (FB F 2337, *1*)

Further distribution in Pakistan Laki of the 'Hala Range' (type locality for both *Cardium halaense* and *C austeni*), Kohat Shales of Kohat, and Bahadur Khel, Khirthar of the Laki Valley, and the 'Alore Hills'

Further distribution Libyan of Egypt, Lower Eocene of Togo(?), Lower Mokattam of Egypt, Upper Mokattam of Egypt, Eocene of the Soudan, and Cyrenaica

Remarks Since Blanford's record from the Khirthar of the Laki Valley was made before the Laki Series was established, it is possible that it may really be of Laki age As Cox has pointed out, other forms from Africa have incorrectly been placed in this species, and some of the records that are not accompanied by illustrations (e g those of Garde and Cuvillier) may not be above suspicion

TRACHYCARDIUM SALTERI (d'Archiac & Haime), 1854

References *Cardium salteri* d'Archiac & Haime, 1854 (pp 259, 367, Pl 23, figs 3*b–d*), Fedden, 1880 (p 203), Cox, 1931*a* (pp 83, 29, 34 (pars)), Cotter, 1933 (p 98)

?*C picteti* d'Archiac & Haime var *minor* d'Archiac & Haime, 1854 (pp 259, 367, Pl 23, figs 3, *a*)

C picteti d'Archiac & Haime, Wynne, 1872 (p 243), Fedden, 1880 (p 203), Heron, 1937 (p 22)

Trachycardium(?) *picteti* (d'Archiac & Haime), A M Davies, 1923 (pars) (p 587)

Very doubtful references *Cardium salteri* d'Archiac & Haime, Medlicott, 1871 (p 17(167)), Oldham, 1893 (p 330), Cox, 1931*a* (pars) (pp 83, 29, 34)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, *2*)

Further distribution in India and Pakistan Probably Laki of the Salt Range, Laki of the 'Hala Range' (type locality), Kohat Shales of Kohat, and Bahadur Khel, Khirthar of Baboa Hill (Cutch), and Kund (3 miles south-west of Kotkai) The very doubtful references refer to the record of the species from the Lakadong Limestone (Ranikot) of Cherrapunji in Assam, the identification seems likely to be incorrect

TRACHYCARDIUM COTTERI (Cox), 1931

References *Cardium ambiguum* J de C Sowerby, 1839 (p 328, Pl 24, fig 2, *non* [illegible]. G Costa, 1839 *antea*), Vickary, 1846 (p 267), d'Archiac, 1850*b* (3, 263, 200), Carter, 1854 (p 251)

C ? *ambiguum* J de C Sowerby, d'Archiac & Haime, 1854 (pp 256, 171, 367)

C ambiguum? J de C Sowerby, Fedden, 1880 (p 203)

?*C greenhoughi* d'Archiac & Haime, L M Davies, 1925 (pp 216, 219)

C greenhoughi? d'Archiac & Haime, L M Davies, 1926*b* (pp 199, 203)

C greenhoughi d'Archiac & Haime, L M Davies, 1926*b* (p 205)

C cotteri Cox, 1931*a* (pp 82, 28, 34, Pl 3, fig 19)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2539, *1*), Upper Chocolate Clays (upper part, local zone 13) (FB F 2520, *2*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2518, *2*), *Kohat area* (*Tarkhobi section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2162, *1*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294, *2*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2291, *2*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *8*, FB F 2255, *6*, FB F 2295, *7*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *1*), Kohat Limestone (local subzone 4*b*) (FB F 2270, *1*), *Kohat area* (*Shekhan Nala section*) Kaladhand Limestone (local subzone 4*a*) (FB F 2334, *2*, FB F. 2335, *4*, FB F 2336, *2*), Upper Kohat Shales (local subzone 4*a*) (FB F 2337, *5*, FB F 2341, *8*, FB F 2342, *1*), *Kohat area* (*Sirki Paila*) Sirki Shale (local subzone 4*d*) (FB F 2106, *1*)

Accessory samples *Kohat area* (*Tarkhobi*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2192, *1*, FB F 2193, *1*), Kohat Shales (local subzone 4*a*) (FB F. 2183, *3*, FB F 2184, *3*), *Kohat area* (*Panoba*) Shekhan Limestone (local zone 3) (FB F 2286, *1*)

Further distribution in Pakistan and India Meting Shales of Western Pakistan; Laki Limestone of Western Pakistan, Ghazij Shales of Hindu Bagh, Laki of the 'Hala Range', Kohat Shales of Kohat, Khirthar of the Mari Hills, and Baboa Hill in Cutch (type locality)

Remarks It appears as if the Meting Shales record requires substantiation Records of the species from Burma by Dalton (1908, pp 636, 612, 613), Cotter (1912, pp 226, 234, 236, Pl 18, figs 5, 8), Cox (1931*a*, p 82), Cotter (1938, pp 69, 70) and Clegg (1938, pp 208, 209, 210, 211), are all from the Yaw Stage, all of them, including Dalton's specimen in the Natural History Museum, are more orbicular than *Trachycardium cotteri*, which also lacks the oblique striae characteristic of *Discors* The Burma form is referable to *Cardium subfragile* Boettger, 1875 *non* d'Orbigny, 1850, which was renamed *Discors kyetubokensis* Eames

TRACHYCARDIUM PSEUDOGIGAS n sp

(Figures 107*a*, *b*, *c*, plate 16)

Material *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1967, the holotype, Reg No L 80263, and 9 topotypes together with 3 fragments, Reg No L 80264–9, FB F 1966, *4*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2572, *1*, FB F 2571, *2*)

Description Shell large, apparently not very thick-shelled for the size, suborbicular in outline, slightly wider than high, rather strongly inflated Umbos distinct, moderately prominent, slightly prosogyrous, submedian in position, if anything situated slightly anterior to the middle line Apart from the umbonal projection, the outline is almost circular, the posterior portion of the shell being very slightly produced and with a subtruncated appearance Antero-dorsal margin not long, arched, merging insensibly with the anterior end Posterior end gently convex, subtruncated, sloping upwards slightly towards the umbos, joining the ventral margin in a regular curve, and forming a rounded, obtuse angle with the postero-dorsal margin Postero-dorsal margin relatively moderately long, almost straight, slightly concave, gently descendent Valve margins internally coarsely fluted Escutcheon short, narrow, lanceolate There is a narrowly cordiform, fairly large, lunular area where the ornament is effaced, the central portion near the umbos is swollen, forming a narrow, pouting area which is separated by a deep incised line on its external side from another arched, curved, swollen band, the distal portion of which fades out after arching round the middle of the central swollen zone Surface of shell ornamented with about 52 closely spaced, flat-topped ribs separated by shallow intervals with a flat base and vertical sides, the width of the intervals being not more than one-third of the width of the ribs, and sometimes distinctly less In some places, especially posteriorly, there is a tendency for the ribs to be a little hollowed out along their middle line Little concentric ornament is to be seen, and the shell was apparently fairly smooth in this respect

Dimensions Holotype length 59 8 mm , height 56 8 mm , thickness (both valves) 41 8 mm One of the topotypes is as much as 70 0 mm in length

Remarks. *Cardium gigas* Defrance as figured by Taeger (1908, p 249, Pl 8, figs 12*a*–*c*), from the Eocene of Hungary, and *C gigas* Defrance var as figured by Taeger (1908, p 250, Pl 8, fig 13), from the Eocene of Hungary, although comparable in size, have less pointed umbos and a more convex ventral margin, *C* (*Trachycardium*) *gigas* Defrance as figured by

Cossmann & Pissarro (1904*a*, Pl 18, figs 69–2, 2′), from the Lutetian of Grignon and Maulette, attains a larger size and is relatively higher *Trachycardium cotteri* (Cox), from the Laki and Khirthar of India and Pakistan, is distinctly smaller and less transverse. *Cardium pharaonum* Cuvillier (1930, p 312, Pl 18, figs 9, 10), from the Ypresian of Egypt, has more numerous and finer ribs *C* (*Loxocardium*) *mayombicum* E Vincent (1913, p 34, Pl 3, figs 27, 28), from the Palaeocene of the Belgian Congo, is very much smaller

Genus *DISCORS* Deshayes, 1858

(*Descr An s Vert Bassin Paris*, **1**, 569)

Type species Quoted as being *Cardium subdiscors* d'Orbigny, Eocene

Synonyms *Lyrocardium* Meek, 1876 (*Rep U S Geol Surv Terr* **9**, 173), type species *Lyrocardium lyratum* (Sowerby), Recent, by tautonymy

Amphicardium von Martens, in Moebius, 1880 (*Beitr Meeresfauna Mauritius Seychellen, Moll* p 324), type species *Cardium* (*Amphicardium*) *lyratum* Sowerby, Recent, monotypy

Divaricardium Dollfus & Dautzenberg, 1886 (*Feuill Jeun Nat* **16**, 95), type species *Cardium discrepans* Basterot, Miocene, Cossmann, 1886

Hemidiscors Rovereto, 1898 (*Atti Soc Ligust Sci Nat* **9**, 163), type species *Cardium rugiferum* Rovereto, Oligocene, original designation

Remarks Deshayes originally mentioned only two species under his subgenus *Discors* *Cardium subdiscors* d'Orbigny and *Cardium parisiense* d'Orbigny, another Eocene species Rovereto, in proposing his new section *Hemidiscors*, finishes his paragraph on p 163 with the words '(tipo = *C hörnesi* Deshayes)', since he is obviously referring to *Cardium rugiferum* in his discussion, and explicitly states that it is the type on a later page, it is concluded that the earlier reference to *C hörnesi* refers to something else or is a mistake

DISCORS BUNBURYI (d'Archiac & Haime), 1854

References *Cardium* sp d'Archiac, 1850*b* (**3**, 265)

C bunburyi d'Archiac & Haime, 1854 (pp 260, 367, Pl 23, figs 7, *a*), Fedden, 1880 (p 203), Vokes, 1937 (p 5)

C (*Discors*) *bunburyi* d'Archiac & Haime, Cox, 1931*a* (pp 83, 28, 34, 35)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 2) (FB F 1835, *1*), Green and Nodular Shales (local zone 5) (FB F 1887, *1*), Green and Nodular Shales (local zone 6) (FB F 1893, *1*, FB F 1899, *1*, Reg No L 80270, FB F 1900, *1*, FB F 1903, *4*), Rubbly Limestones (local zone 6) (FB F 1906, *1*, FB F 1910, *2*, FB F 1912, *2*), Shales with Alabaster (local zone 7) (FB F 1954, *1*), *Pellatispira* Beds (local zone 15) (FB F 1981, *1*), *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2534, *1*), Upper Chocolate Clays (upper part, local zone 14) (FB 2517, *2*, FB F 2516, *2*), *Kohat area* (*Tarkhobi section*) Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *1*), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2292, *2*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294, *1*, FB F 2287, *1*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *1*), Nummulite Shale (local subzone 4*b*) (FB F 2266, *1*), *Kohat area* (*Shekhan Nala section*) Kaladhand Limestone (local subzone 4*a*) (FB F 2335, *3*), *Kohat area* (*Sirki Paila*) Sirki Shale/Kohat Limestone (local subzone 4*d*) (FB F 2114, *4*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2183, *1*)

FURTHER DISTRIBUTION IN PAKISTAN Shekhan Limestone of the Kohat/Bahadur Khel area, Laki of the 'Hala Range' (type locality), Kohat Shales of Harnai, Khirthar of the 'Alore Hills' (Sind)

FURTHER DISTRIBUTION Middle Eocene of Somaliland

DISCORS PUNJABENSIS n sp

(Figures 106*a*, *b*, plate 15)

MATERIAL *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1854, *1*, FB F 1857, *1*, FB F 1858, *2*, FB F 1862, *2*), Green and Nodular Shales (local zone 4) (FB F 1864, *2*, FB F 1867, *2*, FB F 1868, *6*), Green and Nodular Shales (local zone 5) (FB F 1873, *6*, FB F 1885, *1*, FB F 1890, *10*+), Green and Nodular Shales (local zone 6) (FB F 1893, *2*, FB F 1897, *4*, FB F 1899, *2*), Rubbly Limestones (local zone 6) (FB F 1910, *6*), Shales with Alabaster (local zone 7) (FB F 1931, *2*, FB F 1932, the holotype, Reg No L 80271, and 10 topotypes, Reg No L 80272–7, FB F 1935, *6*, FB F 1938, *1*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *1*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *2*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *7*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2291, *5*)

DESCRIPTION Outline surborbicular-suboval, slightly truncated posteriorly, drawn out a little in a postero-ventral direction Inflation moderate Poorly preserved specimens sometimes appear subquadrate in outline, or slightly higher than wide Umbo moderately prominent to very prominent, depending upon the preservation, situated slightly anterior to the middle line The suborbicular-suboval outline is sometimes a little flattened on the anterior and posterior ends and on the ventral margin, giving a subquadrate appearance The posterior truncation is sometimes very vague, and, when present, causes the posterior margin to slope upwards in a very slightly convex curve, that is not far removed from the vertical, to meet the postero-dorsal margin in a rounded obtuse angle, its lower end meeting the posterior end of the ventral margin in a rounded angle little more than a right angle The holotype is more orbicular than such forms Ornament consisting of radial riblets and slightly discordant concentric ornament Riblets at least 75 in number, there being a small anterior zone on which the ribs are effaced or obsolete, anteriorly they are fine and about twice as narrow as their intervals, but these soon grade into broad, flat ribs with linear intervals on the median portion of the shell, the latter are not strongly developed, but grade into stronger, rather raised ribs of a similar type on the posterior area The almost concentric threads are moderately closely spaced, fine and distinct, being about ¼ mm apart antero-ventrally, tend to be effaced medially and on the extreme posterior portion of the shell, are separated by intervals at least four times their width, and are only slightly discordant

DIMENSIONS Holotype length 26 2 mm, height 26 6 mm Topotype length 28 7 mm, height 28 7 mm, thickness (both valves) 19 0 mm

REMARKS The specimens are all moulds *Discors simlaensis* Vokes (1937, p. 4, fig 3), from the Lower Subathu (Khirthar) of the Simla Hills, is less drawn out postero-ventrally (i e more regularly oval), is relatively a little higher, and, moreover, has only 23 ribs which are separated by intervals half as wide as themselves *D kyetubokensis* Eames (1950) (a new name for *Cardium subfragile* Boettger, 1875 *non* d'Orbigny, 1850), from the Yaw Stage of Burma, the Upper Eocene of Java, and Stages *α* and *β* of the Eocene of Borneo, has a somewhat similar number of ribs (more than 68 according to Boetgger, and more than 60 according to Cotter), but the anterior ribs do not seem to become so fine, the shell is more regularly oval, the umbos never high, and, judging from collections made in Burma, it attained a much larger size

DISCORS SORIENSIS n sp

(Figure 83, plate 14)

MATERIAL *Zinda Pir section Pellatispira* Beds (local zone 15) (FB F. 2506, *2*, FB F 2502, the holotype and its impression, Reg No L 80278, FB F 2501, *10*+)

DESCRIPTION Outline suborbicular, slightly drawn out in a postero-ventral direction The umbos appear to have been fairly prominent (although this appearance is probably accentuated by crushing) and to have been situated anterior to the median line at about two-fifths of the length The specimen does not seem to have been very strongly inflated, although here again the crushing the specimen has undergone may have produced a false appearance There are 60 radial ribs, when weathered these appear as flat riblets separated by intervals of the same width, but round the margins of the adult shell where their original appearance is preserved they are seen to be rather vague and separated by linear intervals, they are relatively broader posteriorly than anteriorly Concentric ornament gently but distinctly discordant, consisting of fine, distinct, wide-spaced threads, which are 0 75 to 1 12 mm apart ventrally, and best seen on the anterior part of the shell

DIMENSIONS Holotype length 19 0 mm , height 18 6 mm (crushed specimen)

REMARKS The solitary specimen and its impression are crushed, but the details of the ornament seem sufficiently characteristic for description, the specimen itself is a mould of an external impression *Discors simlaensis* Vokes (1937, p 4, fig 3), from the Lower Subathu (Khirthar) of the Simla Hills, has less uniformly developed ribs, which are, moreover, only 23 in number *D kyetubokensis* Eames (1950) (a new name for *Cardium subfragile* Boettger, 1875 *non* d'Orbigny, 1850), from the Yaw Stage of Burma, the Upper Eocene of Java, and Stages *α* and *β* of the Eocene of Borneo, seems to have more uniformly developed ribs which appear to be fewer at the same stage of growth (there are 55 on a specimen 32 mm high, and at least 60 to 68 in adults), and the discordant concentric ornament is not so distinct, so continuous, or so widely spaced, the Zinda Pir specimen does not attain the large size of *Discors kyetubokensis* *Cardium* (*Divaricardium*) *polyptyctum* Bayan as figured by Oppenheim (1901 *a*, p 163, Pl 16, fig 11), from the Priabonian of Via degli Orti, is higher and more subquadrate *C* (*Discors*) *anomale* Matheron as figured by Rovereto (1914, p. 153, Pl 6, fig 3), from the Oligocene of Liguria, has considerably less widely spaced and stronger discordant ornament The shell appears to have been less inflated, the ribs a little fewer in number, and the discordant threads finer and more widely spaced than in *Discors punjabensis*

DISCORS NEMOCARDIIFORMIS n sp

(Figures 108*a*, *b*, plate 16)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2541, *1*, FB F 2540, the holotype, Reg No L 80279, and 1 topotype, Reg No L 80280), Upper Chocolate Clays (upper part, local zone 14) (FB F 2517, *2*, FB F 2516, *2*)

Description Shell transversely oval-subquadrate, a little wider than high, moderately strongly inflated, a little drawn out in a postero-ventral direction Umbos rather small, not conspicuous, rather narrow and therefore appearing more prominent than they really are, situated slightly anterior to the middle line Anterior end evidently moderately sharply rounded Ventral margin moderately convex The posterior end seems to have been obliquely truncated, fairly straight, sloping upwards markedly towards the umbos, joining the ventral margin in a sharply rounded curve and the postero-dorsal margin in a blunt obtuse angle Postero-dorsal margin short, almost straight, gently descendent Surface ornamented with numerous radial ribs (there must have been at least 60) which are rather flat and separated by linear intervals There are also distinct, moderately closely spaced, slightly discordant threads of which there are 3 in ½ mm ventrally The topotype shows that the young stages were more orbicular and less subquadrate

Dimensions Holotype length 19 0 mm , height 16 4 mm (possibly slightly incomplete), thickness (both valves) 11 5 mm

Remarks *Nemocardium*(?) sp of Cuvillier (1935, p 24, Pl 2, figs 11, 25, 30), from the Upper Lutetian of Egypt, shows some resemblance in form, but is less inflated and a little more drawn out posteriorly *Nemocardium doncieuxi* Cossmann (1921 *a*, p 83, Pl 5, fig 7), from the Cuisian of Gan (Aquitaine), has a somewhat similar outline to the holotype of *Discors nemocardiiformis*, but has a more produced posterior truncated region and lacks the discordant threads of *Discors* *D* *punjabensis* is distinctly larger and less transverse, and has the umbos relatively less swollen *D* *sonensis* is also less transverse and has distinctly more widely spaced discordant threads

Superfamily Veneracea

Family Veneridae

Genus *CLEMENTIA* Gray, 1847

(*Proc Zool Soc Lond* p 184)

Type species *Clementia papyracea* (Gray), Recent, original designation

Synonym *Blainvillia* Hupé, 1854 (*Rev Mag Zool* (2), 6, 219) *non* Robineau-Desvoidy, 1830 (Dipt), type species if not yet selected, to be chosen from the two Recent species *B* *vitraea* (Chemnitz), Recent and *B* *erythraea* Hupé, Recent

Remarks Gray's records of *Clementia* in 1840 (*Syn Cont Br Mus* 42nd ed , p 149) and in 1842 (*Syn Cont Br Mus* 44th ed , p 75) are *nomina nuda*.

CLEMENTIA PAPYRACEA (Gray), 1825

REFERENCES *Venus? papyracea* Gray, 1825 (p. 137)

V non-scripta J de C Sowerby, 1839 (p 327, Pl 23, fig 8), Fedden, 1880 (p 202), Dollfus, 1915 (pp 36, 26, Pl 1, figs 817, 818, 818*a*), Van der Vlerk, 1931 (p 280).

V hyalina R A Philippi, 1849 (p. 39, *Venus*, Pl 10, fig 6)

V non scripta J de C Sowerby, d'Archiac, 1850*b* (3, 262), d'Archiac & Haime, 1854 (pp 246, 247, 366, Pl 17, figs 7, *a*), Carter, 1854 (p 295), Dollfus, 1919 (p 14)

Clementia papyracea (Gray), Gray, 1847 (p 184), G B Sowerby, 1852 (p 700, Pl 151, fig 155), Deshayes, 1853*c* (p 171, Pl 21, fig 1), Deshayes, 1853*a* (p 197), H & A Adams, 1856 (p 433, Pl 109, figs 1, 1*a*), Martin, 1879 (p 99, Pl 17, fig 6), Noetling, 1901 (p 93), Pilgrim, 1908 (p 40), Boettger, in Verbeek, 1908 (pp 684, 669), Martin, 1917 (p 273), Cox, 1927 (p 54, Pl 4, figs 3, 4), Douglas, 1927 (p 10, Pl 13, fig 10), Cox, 1929 (pp 172, 175), Cox, 1930*b* (pp 130, 158, Pl 15, fig 4), Van der Vlerk, 1931 (p 277), Koperberg, 1931 (p 14), Prashad, 1932 (p 262), Cox, 1936 (pp 62, 8, 9, 10, Pl 8, figs 7, 8), Mukerjee, 1939 (pp 23, 90, Pl 1, fig 17), Krishnan, 1943 (pp 452, 453)

C similis G B Sowerby, 1852 (p 700, Pl 151, fig 156), Deshayes, 1853*a* (p 198).

C strangei Deshayes, 1853*b* (p 17)

C moretoniensis Deshayes, 1853*b* (p 18)

Astarte hyderabadensis d'Archiac & Haime, 1854 (pp 242, 366, Pl 16, figs 17, *a*), Blanford, 1876 (p 16), Medlicott & Blanford, 1879*b* (pars) (p 465), Blanford, 1880 (pars) (pp 48, 56), Fedden, 1880 (pars) (p 202), Fedden, 1884 (pp 47, 48), Pilgrim, 1908 (pp 25, 32, 63, 65), Clegg, 1933 (pp 2, 6)

Venus hyderabadensis d'Archiac & Haime, 1854 (pp 247, 366, Pl 17, figs 8, *a*), Fedden, 1880 (p 202), Dollfus, 1915 (p 36)

V astarteoides d'Archiac & Haime, 1854 (pp 247, 366, Pl 18, figs 1, *a*), Pilgrim, 1908 (pp 40, 46), Furon, 1941 (p 363)

V nonscripta J de C Sowerby, Wynne, 1872 (p 265), de Bockh, Lees & Richardson, 1929 (p 111), Furon, 1941 (p 353)

Cyprina compressa Fuchs var Abich, 1882 (p 253, Pl 7, fig 3)

Venus non-scripta? J de C Sowerby, Fedden, 1884 (pp 47, 48, 49)

Mactra hyderabadensis (d' Archiac & Haime), Noetling, 1899 (p 36)

M nonscripta (J de C Sowerby), Noetling, 1899 (p 36)

Sunetta yethama Cotter, 1923 (p 10, Pl 2, fig 8), Fermor, 1932 (p 29), Chhibber, 1934 (p 226)

Astarte(?) sp Cossmann, 1923 (p 120, Pl 7, fig 1)

Clementia non-scripta (J de C Sowerby) var ? Cox, 1924 (p 62, fig 4)

Venus (*Clementia*) *papyracea* Gray, Vredenburg, 1928*b* (p 455, Pl 32, fig 3)

V (*Clementia*) *papyracea* Gray var *grandis* Vredenburg, 1928*b* (p 455, Pl 32, figs 1, 2, 4)

V (*Clementia*) *protopapyracea* Vredenburg, 1928*b* (p 456, Pl 30, figs 9–11)

Clementia cf *papyracea* (Gray), Siemon, 1929 (p 24)

C non-scripta (J de C Sowerby), Van der Vlerk, 1931 (p 277)

Blagraveia(?) *yethama* (Cotter), Cotter, 1938 (p 68)

DOUBTFUL RECORDS The following may refer to either *Clementia papyracea* or to *Blagraveia sindensis* (d'Archiac & Haime)

Tapes nonscripta (J de C Sowerby), Wynne, 1872 (p 245)

Venus astarteoides d'Archiac, Ball, 1874 (p 153)

V hyderabadensis d'Archiac, Ball, 1874 (p 153)

Astarte hyderabadensis d'Archiac & Haime, Medlicott & Blanford, 1879*b* (pars) (p 459), Duncan, 1880 (p 9), Blanford, 1880 (pars) (pp 48, 56), Fedden, 1880 (pars) (p 202)

Venus astarteoides d'Archiac & Haime, Fedden, 1880 (p 202)

MATERIAL *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1966, *5*, Reg No L 80281–5, FB F 1967, *3*), Upper Chocolate Clays (lower part, local zone 12) (FB F 1978, *1*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2733, *2*, FB F 2555, *2*, FB F 2554, *6*, FB F 2731, *2*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2516, *2*), *Pellatispira* Beds (local zone 15) (FB F 2501, *2*)

FURTHER DISTRIBUTION IN PAKISTAN AND INDIA Lower Nari north of Kudini (Baluchistan) (type locality for *protopapyracea*), Gaj of Cutch, Kathiawar, and Sind (Soomrow, in Cutch, is the type locality for *non-scripta*), Boka Bil of Assam, Talar Stage north of the Talar Gorge, Gwadar Stage of the Mekran Coast, Pliocene of Karikal The type localities for *Astarte hyderabadensis*, *Venus hyderabadensis* and *V astarteoides* are in the 'Hala Range'

FURTHER DISTRIBUTION Yaw Stage of Burma (3 miles west-south-west of Yethama is the type locality for *Sunetta yethama*), Oligocene of Oktaberd (Erivan) (*Cyprina compressa* var), Burdigalian of Persia, Lower Miocene of Java, Middle Fars (Vindobonian) of Persia, Middle Miocene of Egypt, and Steirmark (Austria), Upper Miocene of Java, Miocene of Pemba, and Lower Saadang, Pliocene of Zanzibar, the Aru Islands, south-west New Guinea, Timor, Java, and Mugersim Island, Upper Tertiary of the Celebes, Pleistocene of the Red Sea coast, Recent in numerous localities in the Indo-Pacific region, which is the type area (e g Japan, Philippine Islands, Netherlands East Indies, the Malay Archipelago, East Australia, India, the Persian Gulf, and Arabia)

DISTRIBUTION OF DOUBTFUL RECORDS Those records which may refer to either *Clementia papyracea* or to *Blagraveia sindensis* concern specimens from the Eocene of the Luni Pathan Hills, and from the Khirthar of Wagot, and western Sind

REMARKS The species *Clementia papyracea* does not appear to have been recorded under that specific name from beds older than Miocene in age The species is, however, very common in the Oligocene and Miocene of Burma, and prior to 1942 there were in the Burmah Oil Company's collections from these horizons specimens labelled as *C papyracea* by Vredenburg The variety *grandis* Vredenburg appears to be merely a local variant, and not worth retaining as a true variety, specially favourable living conditions seem to have been responsible for the development of forms rather larger than usual, but which occur side by side with, and grade into the normal form *C protopapyracea* (Vredenburg) was believed to differ from *C papyracea* mainly in the concentric folds becoming obsolete ventrally, but this is an inconstant character, seen also in specimens from the Miocene, and which may in some cases be due to wear. *Sunetta yethama* Cotter also appears to be conspecific with *Clementia papyracea*, the pallial sinus being of the usual type The forms here recorded from the Eocene of Pakistan are also conspecific with *C papyracea*, and the pallial sinus is identical with that of the latter species; these forms do not belong to the genus

Blagraveia as they are less inflated and do not possess the two internal plates bounding the lunule—*Sunetta yethama* (which Cotter tentatively placed as a *Blagraveia*) differs from *Blagraveia* in a like manner The writer has seen specimens of *Clementia papyracea* from certain Eocene beds in Cutch which in size, form, ornament, etc , are indistinguishable from specimens from the Gaj It is concluded, therefore, that the species ranges from Middle Eocene to Recent, and that there is no break or gap in its record within these limits.

Genus *BLAGRAVEIA* Cox, 1931

(*Proc Malac Soc Lond* 19, pt 4, p 183)

Type species *Blagraveia corrugata* Cox, Eocene, original designation

BLAGRAVEIA CORRUGATA Cox, 1931

References *Blagraveia corrugata* Cox, 1931*b* (p 184, Pl 21, figs 5, 8, 9), Cox, 1931*a* (pp 82, 28, 34, 35), Cotter, 1933 (p 98)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1899, *1*, FB F 1900, *5*, Reg No L 80286–90), Rubbly Limestones (local zone 6) (FB F 1908, *1*, FB F 1910, *2*, FB F 1912, *2*, FB F 1913, *2*, FB F 1916, *2*, FB F 1917, *10*+), Shales with Alabaster (local zone 6) (FB F 1919, *4*, FB F 2060, *2*), Shales with Alabaster (local zone 7) (FB F 1933, *1*, FB F 1935, *2*, FB F. 1942, *2*, FB F 1954, *6*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2732, *2*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, *1*), *Kohat area* (*Panoba section*) Upper Shekhan Limestone (local subzone 3*b*) (FB F 2291, *6*)

Further distribution in Pakistan Laki of Sind Kohat Shales of Kohat, and Bahadur Khel, Middle Khirthar of Loralai District (Baluchistan), Khirthar of the 'Alore Hills' (Sind)

Further distribution Uppermost Ypresian of Somaliland

Remarks Although here treated as a separate species, it seems possible that *Blagraveia corrugata* may, after all, be a variant of *B sindensis*, the rather truncated appearance of the posterior region being due to distortion during preservation in soft calcareous muds, preservation under such conditions often producing a wide range of curious shapes In well-preserved specimens, however, there does seem to be some constant difference in appearance, and the two forms are best still treated as different species

BLAGRAVEIA SINDENSIS (d'Archiac & Haime), 1854

References *Crassatella* indet , d'Archiac, 1850*b* (3, 258)

C sindensis d'Archiac & Haime, 1854 (pp 234, 365, Pl 16, figs 3, *a*), Ball, 1874 (p 152), Medlicott & Blanford, 1879*b* (p 459), Duncan, 1880 (p 9), Blanford, 1880 (p 48), Fedden, 1880 (p 201)

C halaensis d'Archiac & Haime, 1854 (pp 234, 359, 365, Pl 16, figs 4, *a*), Medlicott & Blanford, 1879*b* (p 459), Duncan, 1880 (p 9), Blanford, 1880 (pp 48, 127), Fedden, 1880 (p 201)

Blagraveia sindensis (d'Archiac & Haime), Cox, 1931*b* (p 185, Pl 21, figs 3, 6, 7, 10, 11), Cox, 1931*a* (pp 82, 28, 34, 35), Cotter, 1933 (p 98)

DOUBTFUL RECORDS. See under *Clementia papyracea*

MATERIAL *Rakhi Nala section* Green and Nodular Shales (local zone 5) (FB F 1886, *1*), Green and Nodular Shales (local zone 6) (FB F 1893, *10*+, FB F 1897, *10*+, FB F 1898, *10*+, FB F 1900, *10*+, FB F 2042, *2*, FB F 1902, *6*, FB F 1903, *6*, Reg No L 80291–6), Rubbly Limestones (local zone 6) (FB F 1904, *1*, FB F 1906, *2*, FB F 1908, *6*, FB F 1910, *1*, FB F 1911, *1*, FB F 1913, *10*+, FB F 1914, *3*, FB F 1915, *1*, FB F 1916, *1*, FB F 1917, *10*+, FB F 1918, *6*), Shales with Alabaster (local zone 6) (FB F 1919, *10*+), Shales with Alabaster (local zone 7) (FB F 1928, *1*, FB F 1931, *6*, FB F 1932, *10*+, FB F 1935, *1*, FB F 1938, *2*, FB F 1940, *6*), Platy Limestone (marker horizon) (FB F 1955, *1*), Lower Chocolate Clays (local zone 10) (FB F 1966, *2*), Lower Chocolate Clays (local zone 11/10) (FB F 1962, *3*), White Marl Band (local zone 11) (FB F 1964, *2*) *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2733, *6*, FB F 2555, *2*, FB F 2554, *6*, FB F 2553, *2*), White Marl Band (local zone 11) (FB F 2734, *6*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, *1*, FB F 2535, *1*, FB F 2534, *2*), *Kohat area* (*Tarkhobi section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2164, *2*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, *15*+, FB F 2172, *6*, FB F 2173, *15*+), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *5*), *Kohat area* (*Panoba section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2293, *1*, FB F 2224, *1*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *4*, FB F 2294, *15*+, FB F 2232, *2*, FB F 2287, *12*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *15*+, FB F 2290, *7*, FB F 2291, *15*+), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *15*+, FB F 2255, *15*+, FB F 2295, *9*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *10*, FB F 2257, *1*), *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2368, *1*, FB F 2312, *1*), Lower Kohat Shales (local subzone 4*a*) (FB F 2331, *1*, FB F 2332, *2*), Kaladhand Limestone (local subzone 4*a*) (FB F 2333, *4*, FB F 2334, *3*, FB F 2335, *1*), Upper Kohat Shales (local subzone 4*a*) (FB F 2341, *6*, FB F 2342, *3*)

Accessory samples *Kohat area* (*Tarkhobi*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2204, *1*), Kohat Shales (local subzone 4*a*) (FB F 2183, *8*, FB F 2184, *15*+), *Kohat area* (*Panoba*) Shekhan Limestone (local zone 3) (FB F 2286, *1*)

FURTHER DISTRIBUTION IN PAKISTAN Meting Limestone of Sind, Ghazij Shales of the Nilawan Ravine, Shekhan Limestone of Kohat, Laki of Sind, Kohat Shales of Kohat, ?Khirthar of the Laki Valley, Eocene of the Luni Pathan Hills The type locality for both *sindensis* and *halaensis* is in the 'Hala Range'

FURTHER DISTRIBUTION Uppermost Ypresian of Somaliland, Middle Eocene of north Persia

DISTRIBUTION OF DOUBTFUL RECORDS See under *Clementia papyracea*

REMARKS Blanford's record from the Khirthar of the Laki Valley was made before the Laki Series was established, and the record may well be of Laki age Records of *Crassatella halaensis* d'Archiac by Frauscher (1886, p 149, Pl 9, figs 1*a*,*b*), and of *C halaensis* d'Archiac var *α* (1886, Pl 8, figs 12*a*,*b*), from the Eocene of the northern Alps, were renamed *Diplodonta ignota* by Schlosser in 1925

Genus *PITAR* Roemer, 1857

(*Krit Unt Art Moll Venus Lin Gm*, *Inaug-Diss*, *Marburg*, p. 15)

Type species *Venus tumens* Gmelin, Recent = *Le Pitar* Adanson ? = *Pitar striatus* (Sowerby), monotypy

Synonyms *Caryatis* Roemer, 1862 (*Malak Bl* 9, 58, 60) *non* Hubner, 1816 (Lepid) (replacement name for *Pitar*)

Pitaria Dall, 1902 (*Proc U S Nat Mus* 26, no 1312, p 353) (*em* for *Pitar*), type species *Venus tumens* Gmelin, Recent, original designation

PITAR(?) *PSEUDOLONGIOR* n sp

(Figures 109 *a*, *b*, plate 16)

Material *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1945, the holotype, Reg No L 80297, and 1 juvenile topotype, Reg No L 80298)

Description Shell transversely oval, strongly inflated, of fairly large size Umbos small for the size of the shell, not at all prominent, prosogyrous, situated well forward at about one-third of the length Antero-dorsal margin somewhat broken on the holotype, apparently of moderate length, slightly convex and rather steeply descendent Anterior end rounded Ventral margin moderately convex, a little less so posteriorly Posterior end rather narrowly rounded Postero-dorsal margin long, slightly convex, gently descendent.

Dimensions Holotype length 48 6 mm (slightly incomplete), height 37 9 mm, thickness (both valves) 29 5 mm

Remarks The two specimens, one of which is a juvenile, are moulds, the form was, however, represented in the Burmah Oil Company's collections prior to 1942, and appears to be worth describing *Meretrix longior* Boussac (1911 *a*, p 221, Pl 14, figs 5, 12), from the Priabonian of the Ravin du Marderic near Chateaugarnier and from the Lattorfian of Lattorf, has larger umbos, is less strongly inflated, and the postero-dorsal margin is more arched

'*PITAR*' *PSEUDOGASTRANA* n sp

(Figures 110 *a*, *b*, 111 *a*, *b*, plate 16)

Material *Rakhi Nala section* Rubbly Limestones (local zone 6) (FB F 1908, *1*), Shales with Alabaster (local zone 7) (FB F 1924, *1*, FB F 1929, *2*, FB F 1930, *6*, FB F 1931, the holotype, Reg No. L. 80299, and 37 topotypes, Reg No L 80300–5, FB F 1932, *6*, FB F 1940, *6*, FB F. 1941, *2*, FB F 1943, *1*, FB F 1944, *4*, F FB 1954, *2*), *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2567, *3*, Reg No L 80428–30), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone *3b*) (FB F 2173, *1*)

Description Shell transversely oval-subtrapezoidal, apparently thin-shelled, moderately well inflated in the anterior and median portions, rather flattened in the caudal region Umbos of moderate size, gently prosogyrous, situated well forward of the middle line at a little more than one-quarter of the length Antero-dorsal margin short, slightly convex, steeply descendent Anterior end rounded Ventral margin convex anteriorly, less convex and subhorizontal medially, almost straight posteriorly, the posterior portion joining the median portion in a very rounded obtuse angle and sloping upwards away from the umbos at an angle of about 45° Posterior end narrowly rounded, subcaudate, situated rather high up Postero-dorsal margin long, straight or almost straight, moderately descendent Lunule and escutcheon not seen Ornament consisting of fine, sharp concentric threads 0 75 to 1 0 mm apart ventrally Pallial sinus narrowly rounded-triangular, its upper part more or less subhorizontal, its apex situated at about half the length of the shell

Dimensions Holotype length 29 0 mm , height 23 0 mm , thickness (both valves) 14 7 mm

Remarks There does not appear to be any closely comparable species in the Eogene literature the writer has consulted The form is most characteristic, and in conjunction with the ornament make the species easily recognizable The form somewhat recalls that of the tellinid genus *Gastrana*, but the Rakhi Nala species is less caudate and the postero-ventral margin is less emarginate The pallial sinus is, however, quite different from that of the genus *Gastrana* which is deep and broadly oval It seems most probable that, if material showing the hinge characters can be found, the species will be discovered to belong to a new genus Resemblance to the genus *Clementia* is not close, the characters of the posterior region and the nature of the ornament and pallial sinus readily distinguishing it

Subgenus *CALPITARIA* Jukes-Browne, 1908

(*Proc Malac Soc Lond* 8, 155)

Type species *Cytherea sulcatana* Deshayes, Eocene, original designation

PITAR (*CALPITARIA*) *RAKHIENSIS* n sp

(Figures 112*a*,*b*, 113*a*,*b*,*c*, 114, plate 16)

Material *Rakhi Nala section* Rubbly Limestones (local zone 6) (FB F 1908, *1*, FB F 1918, *1*), Shales with Alabaster (local zone 6) (FB F 1919, *1*), Shales with Alabaster (local zone 7) (FB F 1925, *6*, FB F 1928, *6*, FB F 1929, *10*+, FB F 2062, *10*+, FB F 1930, *10*+, FB F 1931, *2*, FB F 1932, *2*, FB F 1934, *4*, FB F 1935, *6*, FB F 1938, *10*+, FB F 1941, *1*, FB F 1942, more than 10 syntypes, Reg No L 80314–9, FB F 1943, *10*+, FB F 1944, *10*+, FB F 1948, *4*), Lower Chocolate Clays (local zone 10) (FB F 1966, the holotype, Reg No L 80306, and 7 topotypes, Reg No L 80307–13)

Description Shell of moderate size, high and subtriangular, moderately to moderately well inflated Umbos high, prominent, rather narrow and pointed, prosogyrous, situated distinctly anterior to the middle line at about one-third of the length Escutcheon a narrowly lanceolate, deeply sunken area of moderate length only Lunule a rather indistinct, narrowly cordiform area limited on its outer sides by a fine incised line Antero-dorsal margin short, slightly convex, steeply descendent Anterior end rounded Ventral margin well rounded, a little less convex posteriorly Posterior end moderately narrowly rounded to distinctly narrowly rounded and subcaudate, situated rather low down Postero-dorsal margin rather long, almost straight except near the umbo where it curves over a little, moderately steeply descendent Valve margins internally smooth Pallial sinus narrowly U-shaped, subtriangular, very slightly ascendent, apex rounded and situated half-way across the shell. Ornament consisting of fine but distinct concentric folds with narrow intervals, there being about three folds in ¼ mm There is variation in outline, some forms being considerably more elongate and with a less prominent umbonal region, but still retaining the distinctive subtriangular appearance

Dimensions Holotype length 25 9 mm , height 22 9 mm , thickness (both valves) 13 4 mm One of the topotypes attains a length of 33 2 mm

Remarks This form shows a close resemblance to figs 13 and 14 of *Macrocallista*(?) sp Nagao (1928, p 68(58), Pl 6, figs 3, 13, 14), from the Namazuta fossil bed (Honso Beds) of Japan *Cytherea nitidula* Lamarck as figured by Oppenheim (1906*a*, p 169, Pl 18, fig 5), from the Mokattam Stage of Egypt, is not so high, less triangular, and the umbos are less erect *Pitar quimbrizensis* Caster (1938, p 69, Pl 4, figs 11, 12), from the Eocene of Angola, is less pointed posteriorly, still more convex ventrally, and has larger umbos *Cytherea hungarica* von Hantken as figured by Oppenheim (1896*b*, p 98, Pl 5, fig 2), from the Eocene (Muschellumachelle) of Grancona, has a more curved postero-dorsal margin The Rakhi Nala form bears a superficial resemblance to *Meretrix* (*Tivelina*) *subanaloga* (Dufour) as figured by Cossmann (1906, p 198, Pl 15, figs 20–22), from the Eocene of Bois-Gouët, La Close, and Coislin, but is higher, has a less convex ventral margin, and is somewhat larger The high, subtriangular form of the Rakhi Nala species appears to be characteristic

The pallial sinus is not quite so horizontally disposed or so elongate and tongue-shaped as in *Venus tumens* Gmelin, and is of the type seen in *Cytherea sulcataria* Deshayes, the type of *Calpitaria*, rather than that seen in species referred to *Agriopoma*

PITAR (*CALPITARIA*) *PSEUDOSUBCYRENOIDES* n sp

(Figures 115*a*,*b*, 116, plate 16)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2556, the holotype, Reg No L 80320, and 3 topotypes, Reg No L 80321–3)

Description Shell transversely oval-subtriangular, more subtriangular than suboval, gently to moderately inflated Umbos small, moderately prominent to prominent, prosogyrous, situated a little anterior to the middle line at about three-eighths of the length Antero-dorsal margin of moderate length, slightly convex, gently to moderately descendent Anterior end rather narrowly rounded Ventral margin gently and regularly convex, the curvature being slightly less posteriorly Posterior end narrowly rounded, situated a little lower down than the anterior end Postero-dorsal margin fairly long, gently convex, moderately steeply descendent Details of lunule and escutcheon not preserved Valve margins internally smooth Pallial sinus tongue-shaped, slightly ascendent, triangular, apex narrowly rounded and situated at almost half the length of the shell

Dimensions Holotype length 18 9 mm , height 14 6 mm , thickness (both valves) 7 7 mm One of the topotypes attains a length of 21 4 mm

Remarks The specimens are all internal moulds showing no trace of external ornament *Pitar subcyrenoides* (d'Archiac & Haime) (1854, pp 250, 366, Pl 20, figs 5, 6), from the Upper Khirthar Shales 1 mile north-east of Nili Kach (south of Gumal) and from the Khirthar of Subathu (the type locality), seems to be the most closely related species, but is more inflated umbonally, more triangular in shape on account of possessing more prominent and prosogyrous umbos, and the ventral margin is less regularly convex The pallial sinus is not deep enough for *Pitar* (*sensu stricto*)

PITAR (*CALPITARIA*) *CARTERI* (d'Archiac & Haime), 1854

(Figures 117*a*, *b*, *c*, plate 16)

References *Venus subovalis* d'Archiac, 1850*b* (*nomen nudum*) (3, 262), d'Archiac & Haime, 1854 (pp 248, 366, Pl 18, figs 3, *a*) *non* d'Orbigny, 1850, Ball, 1874 (p 153), Fedden, 1880 (p 202)

Cypricardia carteri d'Archiac & Haime, 1854 (pp 261, 367, Pl 20, figs 14, *a*), Fedden, 1880 (p. 203)

Trapezium [*Cypricardia*] *carteri* (d'Archiac & Haime), A M Davies, 1923 (pars) (p 587)

Cytherea sulcatana Deshayes, Douvillé, 1929 (p 60)

Meretrix cf *sulcatana* (Deshayes), Cox, 1931*a* (pp 30, 28, 34), Cotter, 1933 (p 98)

Material *Rakhi Nala section* Rubbly Limestones (local zone 6) (FB F 1915, *1*), Shales with Alabaster (local zone 7) (FB F 1924, *1*, FB F 1925, *1*, FB F 1928, *2*, FB F 1931, *2*, FB F 1932, *4*, Reg No L 80325–8, FB F 1935, *6*, FB F 1937, *2*, FB F. 1942, *4*, FB. F 1943, *6*, FB F 1944, *2*), Lower Chocolate Clays (local zone 10) (FB F 1967, *1*, Reg No L 80324), *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, *6*), Lower Chocolate Clays (local zone 10) (FB F 2571, *1*, FB F 2569, *1*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, *7*, FB F 2173, *1*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294, *15*+), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *10*, FB F 2290, *1*, FB F 2291, *6*), Kaladhand Limestone (local subzone 4*a*) (FB F 2255, *4*), Upper Kohat Shales (local subzone 4*a*) (FB F 2257, *1*)

Accessory sample *Kohat area* (*Tarkhobi*) Kohat Shales (local subzone 4*a*) (FB F 2184, *3*)

Further distribution in Pakistan Laki of the 'Hala Range' (type locality for both *carteri* and *subovalis* d'Archiac & Haime), Kohat Shales of Kohat, and Bahadur Khel, Khirthar of the Mari Hills, Eocene of the Luni Pathan Hills

Remarks The writer agrees with Cox (1931*a*) that *carteri* and *subovalis* d'Archiac & Haime are conspecific, there being some degree of variation in the species, quite apart from the distortion produced during the compaction of the soft calcareous muds in which the shells were entombed Much depends also upon whether the specimens examined are internal or external moulds, or have the shell preserved. One of the specimens from FB F 1932 agrees very well indeed with the holotype of *carteri*, and the specimen from FB F 1967 (which is here illustrated) has the shell preserved, the ornament well displayed, and is regarded as being conspecific Cox (1931*a*) suggested that *carteri* and *subovalis* d'Archiac & Haime were probably to be identified with *Pitar* (*Calpitaria*) *sulcatana* (Deshayes), of the Paris Basin Eocene, and which is the type species of *Calpitaria* While the pallial sinus of the Pakistan species is closely similar to that of *Calpitaria*, the shell is not so high posteriorly, being subtriangular rather than subquadrate in outline, and the ornament, as displayed by the specimen from FB F 1967, is definitely coarser *Cytherea sulcatana* was figured by Deshayes in 1825 (p 133, Pl 20, figs 14, 15), and the Pakistan forms have been compared with actual specimens in the collection of the Natural History Museum, as well as with Deshayes's illustrations and description. d'Archiac & Haime's specific name *carteri* is not pre-employed, and is therefore retained for the species

C nitidula Lamarck as figured by Oppenheim (1906*a*, p 169, Pl 18, fig 5), from the Mokattam Stage of Egypt, is less elongate, and has higher and less prosogyrous umbos. *C productula* Mayer-Eymar as figured by Oppenheim (1906*a*, p 171, Pl 21, figs 1, 2), from the Libyan Stage of Egypt, is also usually less elongate, and has less erect umbos *Meretrix heluanensis* Cuvillier (1933, p 20, Pl 2, fig 15), from the Lower Mokattam of Egypt, and *Cytherea humata* Locard (1889, p 36, Pl 9, fig 10), from the Eocene of Tunisia, also have higher umbos *C paradeltoidea* Oppenheim (1901 *a*, p 169, Pl 8, figs 2, 2*a*), from the Priabonian of northern Italy, is smaller, more distinctly ornamented, and more elongate anteriorly *C laevigata* Lamarck as figured by Archangelsky (1904, p 109, Pl 6, fig 17, Pl 7, fig 2), from the Palaeocene of the Volga region, has higher and less prosogyrous umbos

Genus *RAKHIA* n g

Type species *Rakhia trapezoidalis* n sp , Lower Eocene

Generic characters Apparently thin-shelled, wider than high, subtrapezoidal in outline, umbos well-marked, distinct, but not prominent or swollen, prosogyrous, situated at about one-third of the length, strong, coarse, concentric folds of the type found in *Blagraveia* and *Clementia* in the umbonal region only, the remainder of the surface with fine, distinct growth lines only Inflation moderate Umbonal slope distinct but not carinate

RAKHIA TRAPEZOIDALIS n g et n sp

(Figures 118*a*, *b*, plate 17)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1853, *1*), Green and Nodular Shales (local zone 4) (FB F 1864, the holotype, Reg No L 80329), Green and Nodular Shales (local zone 6) (FB F 1893, *2*, FB F 1894, *10* +, FB F 1897, *4*, FB F 1898, *1*, FB F 1899, *2*, FB F 1900, *6*, FB F 1903, *4*), Rubbly Limestones (local zone 6) (FB F 1910, *1*, FB F 1912, *2*), Shales with Alabaster (local zone 7) (FB F 1932, *2*)

Description Apparently thin-shelled and not gaping, the appearance of a slight posterior gape on the holotype being produced by crushing Outline transversely trapezoidal Umbos small, sharp, distinct, not swollen or prominent, but a little projecting, gently prosogyrous, situated anterior to the middle line at about one-third or slightly less than one-third of the length Inflation moderate, greater in the umbonal region than ventrally Antero-dorsal margin obscured by matrix, apparently slightly convex, not very long, and gently to moderately descendent Anterior end rounded, rather receding in its lower part Ventral margin gently convex anteriorly where it merges with the anterior end, practically straight posteriorly where it is slightly ascendent Posterior end obliquely truncated, gently convex, sloping upwards distinctly towards the umbos, meeting the ventral margin in a rather sharply rounded curve and the postero-dorsal margin in a well-rounded obtuse angle Postero-dorsal margin partly obscured by matrix, apparently of moderate length only, a little longer than the antero-dorsal margin, fairly straight, gently descendent Strong concentric folds of the type encountered in *Blagraveia* and *Clementia* are present in the umbonal region, where they may be almost 1 5 mm apart, but these soon become effaced, and the greater portion of the surface is smooth except for fine, distinct growth lines Umbonal slope quite distinct, but not carinate, the vague angulation of the line from the umbo to the postero-ventral corner separating off the posterior part of the shell

Dimensions Holotype length 46·4 mm , height 33·6 mm , thickness (both valves—somewhat crushed) 20 1 mm

Remarks In spite of the lack of information concerning the internal characters, the placing of this species in a new genus seems to be justified The writer has encountered no similar species, the form and ornament appearing to be unique The genus is provisionally placed in the Veneridae on account of the apparent lack of any real gape It has been suggested that the species might be a *Panope*, but that genus is thick-shelled, has an anterior and a posterior gape, and a rather different form

Genus *VENERELLA* Cossmann, 1886

(*Ann Soc Roy Malac Belg* **21**, 105)

Type species *Venerupis hermonvillensis* Deshayes, Eocene, Crosse, 1886

VENERELLA PARVA n sp

(Figures 119*a*, *b*, plate 17)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, the holotype, Reg No L 80330, and 3 topotypes, Reg No L 80331–3)

Description Shell small, transversely broadly oval-subtriangular, inflation moderate Umbos small, distinct, moderately prominent, distinctly prosogyrous, situated slightly anterior to the middle line Antero-dorsal margin not very short, straight, moderately descendent Anterior end rounded Ventral margin convex, forming a regular curve with the anterior end Posterior end rounded, degree of rounding variable, broad on the holotype, narrower on some of the topotypes, when it is situated moderately high up Postero-dorsal margin of moderate length, slightly convex, gently to moderately descendent Shell apparently ornamented with fine concentric threads Valve margins internally smooth Pallial sinus broadly V-shaped with a rounded apex, its dorsal part subhorizontal, its ventral branch sloping downwards only slightly towards the posterior end, its apex behind the middle of the shell at about two-fifths of the length

Dimensions Holotype length 11 0 mm , height 9 2 mm , thickness (both valves) 6 0 mm

Remarks The specimens are either moulds or partly decorticated *Meretrix* cf *lunularia* Deshayes as figured by Cuvillier (1935, p 23, Pl 3, figs 17, 18), from the Bartonian of Egypt, is larger, higher posteriorly, and the dorsal margin is more elevated *Cytherea mayeri* Netschaew (1897, p 108, Pl 3, figs 7*a*, *b*, 8*a*, *b*, 8′), from the Eocene of the Volga region, is less equilateral, more elongate posteriorly, and higher and less pointed posteriorly The pallial sinus is unlike that of *Venus tumens* Gmelin, the type of the genus *Pitar*, and seems most like that of the genus *Venerella*

Genus *MACROCALLISTA* Meek, 1876

(*U S Geol and Geogr Surv Terr Rep* **9**, 179)

Type species. *Venus gigantea* Gmelin, Pliocene-Recent = *Macrocallista nimbosa* (Solander), original designation and monotypy

Subgenus *COSTACALLISTA* Palmer, 1927

(*Palaeontogr Amer* 1, no 5, pp 73, 84)

Type species *Callista erycina* (Linné), Recent, original designation

Synonym *Callista* (Poli, 1791) Mörch, 1853 (*Cat Yoldi*, 2, 27) *non* Leach, in Gray, 1852 (Moll), type species *C erycina* (Linné), Recent, Stoliczka, 1871

Remarks Leach, in Gray, referred to *Calista* Poli, which has to be taken as a misprint or a mistake for *Callista*

MACROCALLISTA (*COSTACALLISTA*) *PUNJABENSIS* n sp

(Figures 84*a*, *b*, plate 14, figures 120*a*, *b*, plate 17)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2522, *1*, Reg No L 80341), Upper Chocolate Clays (upper part, local zone 13) (FB F 2520, the holotype, Reg No L 80334, and 9 topotypes, Reg No L 80335–40, FB F 2519, *6*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2517, *2*, FB F 2516, *2*), FB F 2513, *2*, FB F 2511, *1*)

Description Shell transversely subelliptical in outline, a little less high posteriorly, moderately thick-shelled, moderately inflated Umbos rather small, not very prominent, prosogyrous, situated anterior to the middle line at about one-third of the length Escutcheon not observed, apparently extremely narrow Lunule fairly large, narrowly cordiform, limited by an obtuse ridge on the inner side of which it is a little sunk, slightly pouting medially, lacking the strong ornament of the rest of the surface Antero-dorsal margin relatively moderately long, straight, moderately descendent Anterior end rather narrowly rounded, its lower curvature being rather pronounced and giving it a slightly upturned appearance Ventral margin distinctly convex in its anterior and median portions, less so posteriorly Posterior end a little produced, narrowly rounded Postero-dorsal margin long, very slightly convex, gently descendent Ornament consisting of somewhat irregular, fine concentric folds of about the same width as, or slightly narrower than their intervals, there are four folds in 1 5 mm near the antero-ventral margin The valve margins are internally smooth, and a small specimen from FB F 2522 shows the characteristic *Costacallista* type of pallial sinus

A right valve shows the following hinge characters AI and AIII present, separated by a socket for AII, fairly close to the cardinal teeth, AIII less prominent and less elongate than AI and situated above the proximal part of AI *3a* broken 1 vertical as a whole, its anterior margin concave, subtriangular in shape, its anterior part prominent, its postero-ventral part bevelled off *3b* very deeply bifid, not markedly oblique The ligament area is long and excavated, and is limited by a ridge from the furrow separating it from *3b*

Dimensions Holotype length 30 2 mm , height 20 2 mm , thickness (both valves) 12 3 mm

Remarks *Callista elongatotrigona* Newton (1922, p 88, Pl 9, figs 1–5), from the Eocene of Nigeria, is less elongate, and has more prominent umbos *Meretrix* (*Callista*) *montensis* Cossmann as illustrated by Traub (1938, p. 61, Pl 4, figs 6*a*, *b*), from the Palaeocene of Austria, is less elongate and higher along a line passing through the umbos. *Cytherea* *beyrichi* Semper as figured by Wolff (1897, p 253, Pl 23, fig 9), from the Oligocene of Tolz (south Bavaria), has more forwardly placed umbos, coarser ornament, and is less elongate *Callista heberti* Deshayes as figured by Cossmann (1921*a*, p 55, Pl 3, figs 37–40), from the Auversian of Pédelay, and by Cossmann & Pissarro (1904*a*, Pl 10, fig 50–3), from the Lutetian of Trye and from the Bartonian, is less elongate and the ornament more distinctly callistiform *Meretrix* (*Callista*) *suberycinoides* (Deshayes) as figured by Cossmann & Pissarro (1904*a*, Pl 10, fig 50–4), from the Lutetian of Vaudancourt and from the Bartonian, is distinctly less produced posteriorly, has more conspicuous ornament, and is somewhat larger *Cytherea gruneri* Oppenheim (1915, p 33, Pl 2, fig 10), from the Eocene of Togo, is higher *C pseudopetersi* Taeger (1908, p 255, Pl 9, figs 2, 3), from the Eocene of Hungary, is much smaller, less pointed posteriorly, and higher *C dixoni* Deshayes as figured by Frauscher (1886, p 201, Pl 7, fig 5), from the Lower Eocene of the northern Alps, has higher umbos and a more strongly descendent postero-dorsal margin

Genus *PELECYORA* Dall, 1902

(*Proc U S Nat Mus* 26, no 1312, p 346)

Type species *Cytherea hatchetigbeensis* Aldrich, Eocene, original designation

Synonym *Sinodia* Jukes-Brown, 1908 (*Proc Malac Soc Lond* 8, 151), type species *Dosinia trigona* (Reeve), Recent, original designation

Subgenus *CORDIOPSIS* Cossmann, 1910

(*Act Soc linn Bordeaux*, 64, 387)

Type species. *Venus incrassata* Sowerby, Oligocene, original designation

PELECYORA (*CORDIOPSIS*) *INCRASSATA* (J Sowerby), 1817

References *Venus meroe* Linné, Solander in Brander, 1766 (p 41, Pl 8, figs 104, 105)

V incrassata J Sowerby, 1817 (2, Pl 155, figs 1, 2), Nyst, 1843 (Pl 13, fig 6), Nyst, 1845 (pp 181, 640), Bellardi, 1852 (p 239), Abich, 1882 (p 289, Pl 2, figs 8, 8*a*), Bittner, 1884 (p. 440), Alimen, 1936 (p 158)

Cytherea incrassata (J Sowerby), Deshayes, 1825 (p 136, Pl 22, figs 1–3), d'Archiac, 1846 (p 208), Hébert & Renévier, 1854 (pp 195, 217, 223), Forbes, 1856 (p 153, Pl 4, fig 10, Pl 3, fig 10), Deshayes, 1858 (p 454), d'Archiac, 1859*b* (p 788), Guembel, 1861 (pp 604, 606, 610, etc), Hauer & Stache, 1863 (p 614), Sandberger, 1863 (p 300), Goldfuss, 1863 (p. 229), Giebel, 1866 (p 80), von Koenen, 1866 (p 290), Guembel, 1867 (pp 35, 44), von Koenen, 1868*a* (pp 258, 275), von Koenen, 1868*b* (p 170), Mayer, 1869 (pp 364, 372, 373), Fuchs, 1870 (p 184), von Hantken, 1872 (p 88), Fuchs, 1874 (p 132), von Hantken, 1878 (p 236), Wiechmann, 1879 (p 9), Tournouer, 1879 (p 482), Speyer, 1884 (Pl. 5, figs 14–16); Cossmann & Lambert, 1884 (pp 8, 11, 12, 13, 15, 38, 41, 50, 59), G Vincent, 1886*a* (p 15), C Mayer-Eymar, 1887 (p 99), Lienenklaus, 1889–90 (pp 104, 168); Renévier, 1890 (p 386); Förster, 1892 (p 257, Pl. 16, fig 12), Dreger, 1892*b* (p. 339), Mayer-Eymar, C., 1893 (pp 19, 20, 23, 26); Sokolow, 1893 (p 185), von Koenen, 1894 (pp 1259, 1249, Pl 86, figs 12, 13, Pl 87, figs 1–3), Koch, 1894 (pp 326?, 347, 383); Philippson & Oppenheim, 1894 (pp 811, 813, 814), Oppenheim, 1896*c* (pp 267, 274), Kissling, 1896 (pp 54, 7, 8, 9, 10, 11, 13, 17, Pl 6, figs 1–5), Raulin, 1896 (p 550), Penecke, 1897 (p 49), Wolff, 1897 (pp 252, 297, 299, 300, 308, Pl 23, figs 13, 14), Boeck, 1899 (p 1, Pl 7, figs 3*a*,*b*), Deninger, 1901 (p 240), Oppenheim, 1901*a* (pp 295, 306, 316, 321), Oppenheim, 1902 (p 277), Oppenheim, 1903*b* (pp 184, 132, 135, 221), Dreger, 1903 (pp 275, 283), Oppenheim, 1906*b* (p 168), Oppenheim, 1906*a* (p 173, Pl 19, fig 24), Canestrelli, 1908 (p 71), Dollfus, 1909 (table opp p 24), Kranz, 1910 (pp 219, 194, 196, 198, text-figs 2*a*–*d*), Michailovski, 1912 (p 132), Weithofer, 1918 (pp 17, 18, 19, 20, 51, 52, 74, 76, 88, 89, 94, 97), Oppenheim, 1918 (p 3), Oppenheim, 1922 (pp 96, 97), Bourcart, 1922 (pp 76, 77), Schlosser, 1922 (pp 267, 281, 287, 291), Dalloni, 1924 (p 290), Schlosser, 1925*b* (pp 25, 46, 50, 54, 55, 56), Zinndorf, 1928 (p 10), Gočev, 1933*b* (pp 185, 204, 195, 198, 210, Pl 6, figs 3, 3*a*), Abrard, 1933 (p 468), Vialov, 1934*a* (p 144), Alimen, 1936 (pp 10, 34, 37, 38, 40, etc), Baumberger, 1938 (p 388, Pl 27, fig 12), Denizot, 1940 (pp 25, 27, 29, 30, 37), Gorges, 1941 (p 168(54))

C incrassata (J Sowerby) var B Nyst & Westendorp, 1839 (p 8)

Venus suborbicularis Goldfuss, 1841 (p 247, Pl 148, fig 7), R A Philippi, 1851 (pp 48, 84)

V sublaevigata Nyst, 1843 (Pl 12, fig 1), Nyst, 1845 (pp 166, 182)

V incrassatoides Nyst, 1843 (Pl 13, fig 7), Nyst, 1845 (p 182)

Cytherea braunii Agassiz, 1845 (p 41, Pl 13, figs 1–4)

C verneuili d'Archiac, 1846 (p 189, Pl 7, fig 10)

C incrassata Lamarck var J Sowerby, d'Archiac, 1846 (p 208)

C incrassata (J Sowerby) var ? d'Archiac, 1850*a* (pp 430, 453)

Venus incrassata J Sowerby var *striaca* Rolle, 1859 (pp 197, 201, Pl 1, fig 3)

V suessi Michelotti, 1861 (p 59, Pl 6, figs 6, 7)

C incrassata (J Sowerby) var *lunulata* Sandberger, 1863 (p 300, Pl 24, figs 1, 1*a*,*b*)

C incrassata (J Sowerby) var *globularis* Sandberger, 1863 (p 300, Pl 23, figs 11, 11*a*), Foldvari, 1929 (p 38)

C incrassata (J Sowerby) var *obtusangularis* Sandberger, 1863 (p 300, Pl 24, figs 2, 2*a*), Kranz, 1910 (pp 219, 196)

C incrassata (J Sowerby) var *solida* Sandberger, 1863 (p 300, Pl 24, fig 3)

C incrassata Deshayes, von Schauroth, 1865 (p 214), Andreae, 1884 (pp 184, 185, 288), Frauscher, 1886 (pp 201, 251), Oppenheim, 1896*b* (pp 143, 150)

Meretrix incrassata (J Sowerby), Lowry, 1866 (p 210), Newton, 1891 (p 64), Cossmann, 1891*b* (p 275), Harris & Burrows, 1891 (pp 35, 36, 37, 39), Oppenheim, 1900*c* (p 275), Dollfus, 1909 (p 15), Boussac, 1911*a* (pp 218, 414, Pl 12, fig 25, Pl 13, figs 10, 12, Pl 14, figs 1–4, 9–11), Károly, 1914 (pp 44, 61, 62, 66, Pl 5, figs 10, 11), K Roth von Telegd, 1915 (pp 53, 71, 72, 77, Pl 5, figs 10, 11), Fabiani, 1915 (pp 173, 175, 266, 269, 272, 273), Lukovitch, 1926 (p 39), Cuvillier, 1930 (p 199), Soyer, 1931 (pp 201, 202), Venzo, 1933 (pp 214, 216), Soyer, 1935 (p 210), Flandrin, 1938 (p 144), Furon, 1941 (pp 345, 370), Rossi, 1942 (pp 178, 116, 122, Pl 10, fig 10), Furon & Soyer, 1947 (Pl 29, fig 50–43)

Cyprina brevis Fuchs, 1870 (p 64, Pl 11, fig 1)

C compressa Fuchs, 1870 (p 64, Pl 11, figs 2, 3)

Cytherea incrassata (J Sowerby) var *transilvanica* Hofmann, 1870 (p 22, Pl 3, figs 2*a*,*b*,*c*), Koch, 1894 (p 391)

C incrassata (J Sow)?, Tournouer, 1872*a* (p 511)

C incrassata (J Sowerby) var *obtusangula* Sandberger, Speyer, 1884 (Pl 5, figs 17, 18, Pl 6, figs 1–5)

C incrassata (J Sowerby) var *ovalis* Sandberger, Andreae, 1884 (pp 181, 176)

Meretrix bartonensis Edwards MSS, Newton, 1891 (pp 63, 64)

Venus (*Cytherea*) *incrassata* J Sowerby, Mallada, 1892 (p 219)

Cyprina scutellaria Deshayes, Dreger, 1892*a* (pp 274, 275)

Cyprina cf *lunulata* Deshayes, Dreger, 1892*b* (pp 274, 275)

Meretrix (*Amiantis*) *incrassata* (J Sowerby), Rovereto, 1898 (p 184), Dalloni, 1917 (p 114)

M (*Cordiopsis*) *incrassata* (J Sowerby), Rovereto, 1900 (p 100, Pl 7, fig 5), Rovereto, 1914 (p 155, Pl 5, fig 3), Cox, 1931*a* (pp 81, 28, 32, 34, 35, Pl 4, figs 7*a*,*b*), Gillet & Théobald, 1936 (pp 52, 71), Venzo, 1938 (pp 196, 191, Pl 9, figs 12, 13), Venzo, 1939 (p 92), Venzo, 1941 (pp 187, 205, 207, Pl 2, fig 10)

M (*Amiantis*) *incrassata* (J Sowerby) var *obtusangula* Sandberger, Rovereto, 1900 (p 101)

Amiantis incrassata (J Sowerby) var *suessi* (Michelotti), Sacco, 1900 (p 21, Pl 4, fig 31)

A incrassata (J Sowerby) var *trapezoidalis* Sacco, 1900 (p 21, Pl 4, fig 32)

A incrassata (J Sowerby) var *ovoidalis* Sacco, 1900 (p 21, Pl 4, fig 33)

Cytherea cf *incrassata* (J Sowerby), Oppenheim, 1901*a* (p 167, Pl 15, fig 10), Taeger, 1908 (p 259, Pl 9, fig 10)

Meretrix cf *incrassata* (J Sowerby), Fabiani, 1908 (p 203), Toniolo, 1909 (p 288, Pl 25, fig 7)

Cytherea sp Taeger, 1908 (p 258, Pl 9, fig 9)

Dosinia (*Sinodia*) *incrassata* (J Sowerby), Jukes-Browne, 1908 (p 152, Pl 6, fig 2)

Cordiopsis incrassata (J Sowerby), Cossmann & Peyrot, 1910 (p 387), Newton, 1922 (p 85, Pl 9, figs 15–17), Jackson, 1926 (pars) (pp 349, 371), Wrigley, 1929*b* (p 105), Venzo, 1938 (pp 184, 188, 189)

Cytherea incrassata (J Sowerby) var *triangularis* Sandberger, Kranz, 1910 (pp 219, 196)

C incrassata (J Sowerby) var *ovisimilis* Kranz, 1910 (pp 219, 196, text-fig 2*e*)

C incrassata (J Sowerby) var *oblonga* Kranz, 1910 (pp 219, 196, text-fig 2*f*)

Meretrix (*Cordiopsis*) cf *incrassata* (J Sowerby), Cossmann & Peyrot, 1910 (p 407, Pl 17, figs 5, 7, Pl 18, figs 14–16, 30)

Cytherea incrassata (J Sowerby) var Newton, 1911 (p 637), Alimen, 1936 (p 281, Pl 7, figs 1–3)

Meretrix verneuili (d'Archiac), Boussac, 1911*b* (p 82, Pl 21, figs 7–9)

M incrassata (J Sowerby) form *nana* Fabiani, 1915 (pp 107)

Cytherea incrassata (J Sowerby) var *transsylvanica* Hofmeyer, Weithofer, 1918 (p 95)

Cordiopsis cf *incrassata* (J Sowerby), Cossmann, 1921*a* (p 54)

C verneuili (d'Archiac), Cossmann, 1921*a* (p 54, Pl 3, fig 41)

Meretrix (*Sinodia*) *incrassata* (J Sowerby), Dukooizen, 1924 (p 10)

Cytherea (*Amiantis*) *incrassata* (J de C Sowerby), Vredenburg, 1928*b* (p. 451)

C. (*Meretrix*) *incrassata* (J Sowerby), Foldvári, 1929 (p 38), J Noszky, 1939 (p 69)

Meretrix (*Cytherea*) *incrassata* (J Sowerby), Cuvillier, 1930 (p 272), Alimen, 1936 (p. 178); Furon & Soyer, 1947 (p 193)

M *ovisimilis* (Kranz), Cox, 1934 (p 351, Pl 18, figs 6*a*,*b*), Blanckenhorn, 1935 (p 159)

Cytherea incrassata Brongniart, Tomor-Thirring, 1935 (p 9).

Meretrix incrassata Solander, J Noszky, 1936 (pp 89, 94), Gaál, 1938 (pp 12, 56)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *ovalis* Sandberger, Gillet & Théobald, 1936 (p 52, Pl 3, fig 9)

Cythereaincrassata (J Sowerby) var Alimen, 1936 (p 68)

Cythereaincrassata (J Sowerby), Alimen, 1936 (p 69)

Cytherea incrassata (J Sowerby) var *minor*, Alimen, 1936 (p 95)

Meretrix (*Cordiopsis*) *incrassata* (J Sowerby) var *ovisimilis* Kranz, Venzo, 1938 (pp 196, 191), Venzo, 1939 (p 92, Pl 5, figs 27, 28)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *suessi* (Michelotti), Venzo, 1938 (pp 196, 191), Venzo, 1939 (p 92, Pl 5, fig 32)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *ovoidalis* Sacco, Venzo, 1938 (pp 196, 191), Venzo, 1939 (p 92, Pl 5, fig 26)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *obtusangula* Sandberger, Venzo, 1938 (pp 196, 191), Venzo, 1939 (p 92, Pl 5, figs 29, 30)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *compressa* (Fuchs), Venzo, 1938 (pp 196, 191), Venzo, 1939 (p 92, Pl 5, figs 35, 35*a*)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *oblonga* Kranz, Venzo, 1939 (p 92, Pl 5, figs 21–23, 24, 25), Venzo, 1941 (pp 187, 205, Pl 2, fig 11)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *obliqua* Venzo, 1939 (p 92, Pl 5, fig 31)

M (*Cordiopsis*) *incrassata* (J Sowerby) var *obliquissima* Kranz, Venzo, 1939 (p 92, Pl 85, fig 32)

Cytherea (*Meretrix*) *incrassata* (J Sowerby) var *ovoidalis* Sacco, J Noszky, 1939 (p 70)

C (*Meretrix*) *incrassata* (J Sowerby) var *oligolonga* Sacco, J Noszky, 1939 (p 70)

Pitaria incrassata (J Sowerby), Albrecht & Valk, 1943 (pp 133, 145, 151, 154, Pl 14, figs 443–445)

INCORRECT REFERENCES *Cytherea* (*Meretrix*) *incrassata* (J Sowerby) var *koeneni* J Noszky, 1939 (pp 69, 124, Pl 3, fig 3)

MATERIAL *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1954, *31*, Reg No L 80342–7)

FURTHER DISTRIBUTION IN PAKISTAN AND INDIA Ghazij Shales of Hindu Bagh, Gaj of Buta (Cutch), west-south-west of Mhur (Cutch), and Aio-bett hillock (south of Buta, Cutch)

FURTHER DISTRIBUTION The species is of common occurrence and has both a wide geographical distribution and a long vertical range, the following is a summary of its distribution Middle Eocene of Nigeria, Upper or Middle Eocene of Sirtica, Upper Mokattam of Egypt, Lower Bartonian of Switzerland, Upper Eocene of the Caucasus, Bulgaria, and the Bavarian Alps, Eocene of Germany, Hungary, the Aral Sea area, France, Belgium, and Casakstan, Priabonian of Hungary, Italy, and France, Oligocene or Eocene of the Tyrol, Headon Beds of England (Brockenhurst is the type locality), Lower Tongrian of Italy, Lattorfian of north Germany, south Limburg, and Belgium, Tongrian of France, Bembridge Beds of England, Rupelian of France, Italy, Belgium, south Limburg, south

Bavaria, Bernese Jura, Mayence, Switzerland, Hungary, and Dalmatia, Chattian of Italy, Germany, south Limburg and Hungary, Oligocene of Palestine, Polschitza (Krain), Albania, north-west Thessaly, north Syria and Algeria, Miocene or Oligocene of Spain, Schio Beds of Italy, Aquitanian of north Greece, Lower Miocene of Mayence and Persia, the Sables de Morigny of the Paris Basin, the Sables de Voort, the Sables de Boncelles, and the Sables de Berg of Belgium

Remarks J Noszky's (1939) illustration of *Cytherea* (*Meretrix*) *incrassata* var *koeneni* from the Rupelian of Hungary shows a form that is apparently much too elevated and narrow to belong to the species The age of the Rakhi Nala occurrence appears to be highest Lower Eocene, and would thus be the lowest known record of the species The writer follows Stewart (1930) in regarding *Cordiopsis* as a subgenus of *Pelecyora*

Genus *DOSINIA* Scopoli, 1777

(*Introd ad hist nat sist gen lapid*, *plant et an* p 398)

Type species *Chama dosin* Adanson, Recent = *Dosinia africana* (Gray), Herrmannsen, 1847

Synonyms *Pectunculus* Da Costa, 1778 (*Brit Conch* p 183), type species *P capillaceus* Da Costa, Recent, Jukes-Brown, 1911

Arthemis Poli, 1791 (*Test Sicil* 1, Introd p 30) (not binomial)

Cytherea Bolten, in Roding, 1798 (pars) (*Mus Bolt* pt 2, p 177)

Arctoe Risso, 1826 (*H N Europe*, 4, 361), type species if not yet selected, to be chosen from *A nitidissima* Risso, Recent, *A fulva* Risso, Recent, *A lineolata* Risso, Recent, *A reticulata* Risso, Recent, *A parckinsonia* Risso, fossil, and *A punctata* Risso, subfossil

Exoleta Brown, 1827 (*Ill Conch Gr Brit and Ir*, Pl 20, fig 2), type species if not yet selected, to be chosen from the three Recent species *E orbiculata* Brown, *E lincta* (Pulteney), and *E radula* Brown

Artemis Conrad, 1831 (*Amer Mar Conch* p 55, Pl 12) *non* Kirby & Spence, 1828 (Lepid), type species *A concentrica* (Gmelin), Recent, monotypy

Cerana Gistl, 1848 (*Nat Thierr* p viii) (*em pro Artemis*)

Ampithaea Leach, in Gray, 1852 (*Syn Moll Gr Brit* p 312), type species *A exoleta* (Lister), Recent, monotypy

Amphithaea Dall, 1902 (*Proc U S nat Mus* 26, 346) (*em pro Ampithaea*)

DOSINIA RAKHIENSIS n sp

(Figures 121 *a*, *b*, plate 17)

Material *Rakhi Nala section* Green and Nodular Shales (local zone 6) (FB F 1900, the holotype, Reg No L 80348, and 10 topotypes, Reg No L 80349–54, FB F. 2041, *1*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *2*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2294, *15*+, FB F 2232, *1*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *1*, FB F 2291, *12*), Kaladhand Limestone (local subzone 4*a*) (FB F 2254, *7*, FB F 2295, *4*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *2*)

Description Outline suborbicular to subquadrate, a little produced postero-ventrally. Inflation not strong Umbos very forwardly situated, usually at less than a quarter of the length of the shell, small, pointed Antero-dorsal margin short, gently convex, very steeply descendent Anterior end broadly rounded Ventral margin convex, not quite so rounded as the anterior end Posterior end gently convex, appearing subtruncate and sloping upwards a little away from the umbos on the holotype, forming very rounded angles with the ventral and postero-dorsal margins Postero-dorsal margin long, gently convex, subhorizontal in its proximal part, gently descendent distally The ornament is not preserved on the holotype, but one of the topotypes shows traces of the normal type of distinct concentric thread found in *Dosinia* Valve margins internally smooth Pallial sinus very deep and narrowly triangular, its apex beneath the umbo, its upper portion a little concave on the dorsal side The outline of the shell is somewhat variable, some specimens being more elongate than the holotype

Dimensions Holotype length 28 6 mm , height 26 8 mm , thickness (both valves) 11 1 mm One of the topotypes attains a length of 34 6 mm

Remarks The specimens are all moulds which, however, give a good indication of the variation of the form *Nucula* [*Lucina*] *dollfusi* (Cuvillier) as figured by Cuvillier (1930, p 310, Pl 18, fig 12, 1933, p 10, Pl 3, figs 5, 6), from the Upper Mokattam of Egypt, is more transversely oblique, and its general form and outline suggest that it also is a *Dosinia*

Superfamily SOLENACEA

Family SOLENIDAE

Genus *SOLEN* Linné, 1758

(*Syst Nat* 10th ed p 672)

Type species *Solen vagina* Linné, Recent=*S brevis* Gray, Children, 1822

Synonyms *Hypogaea* Poli, 1791 (*Test Sicil* 1, Introd p 29) (not binomial)

Hypogaeoderma Poli, 1795 (*Test Sicil* 2, 251, 257) (not binomial)

Solenarius Dumeril, 1806 (*Zool Anal* p 168) (genus without species)

Vagina Megerle von Muhlfeld, 1811 (*Ges Nat Fr Berlin Mag* 5, 44), type species *Vagina recta* (Linne), Recent, monotypy

Listera Leach, in Gray, 1852 (*Syn Moll Gr Brit* pp 259, 261) *non* Turton, 1822 (Moll) *nec* Meneghini, 1843 (Coel), type species *L vagina* (Linné), Recent monotypy

Fistula (Martini, 1774) Morch, 1853 (*Cat Yoldi*, 2, 6) *non* Oken, 1815 (Spong), type species if not yet selected, to be chosen from the following four Recent species *Solen zeylanicus* Leach, *S brevis* Gray, *S corneus* Lamarck and *S scalprum* 'Broderip' d'Orbigny

SOLEN PSEUDOMANENSIS n sp

(Figure 122, plate 17)

Material *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 14) (FB F 2513, the holotype, Reg No L 80355)

Description Shell subrectangular in outline, not very elongate for the genus, approximately three times as long as high Umbo small and inconspicuous, practically terminal at the anterior end Dorsal margin long and quite straight Posterior end vertical as a whole, gently convex, meeting the adjacent margins in rounded curves Ventral margin parallel to the dorsal margin, horizontal Anterior end subvertical as a whole, but distinctly more convex than the posterior end Growth lines exceedingly fine, their change in direction marked by a very vague furrow running from the umbo to the postero-ventral corner

DIMENSIONS Holotype length 17 3 mm , height 6 2 mm

REMARKS The single specimen is an impression *Solen manensis* Cotter (1923, p 5, Pl 1, figs 1*a*,*b*), from the Yaw Stage of Burma, is relatively a little more elongate and slender, and is also slightly arched *Solen priabonensis* Vinassa de Regny (1898, p 182, Pl 20(7), figs 1*a*,*b*), from the Priabonian of Italy, is larger and still less elongate

Family CULTELLIDAE

Genus *SOLECURTUS* Blainville, 1824

(*Dict Sci Nat* **32**, 351)

TYPE SPECIES *Solecurtus strigilatus* Blainville, Recent = *Solen strigillatus* Linné, Anton, 1839

SYNONYMS *Psammobia* Risso, 1826 (*Hist nat Europe merid* **4**, 375) (pars)

Psammosolen Risso, 1826 (*Hist nat Europe merid* **5**, 385), type species *Psammobia strigillata* (Linné), Recent, Dall, 1900

Macha Oken, 1835 (*Allg Naturges* **5**, pt 1, p 298), type species *Solen strigilata* Linne, Recent, monotypy

Solenocurtus Sowerby, 1842 (*Conch Man* 2nd ed , p 262) (*em*)

Cyrtosolen Herrmannsen, 1848 (*Indicis Gen Malac* **2**, 468) (*em*)

Adasius Leach, in Gray, 1852 (*Syn Moll Gr Brit* pp 264, 266), type species *Solen strigilatus* Linné, Recent = *Adasius loscombeus* Leach, in Gray, original designation

Psamosolen Woodring, 1925 (*Contrib Geol Paleont W Indies, Mioc Moll Bowden*, p 182) (error)

SOLECURTUS SORIENSIS n sp

(Figure 123, plate 17)

MATERIAL *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 14) (FB F 2513, the holotype, Reg No L 80356, and 1 topotype, Reg No L 80357)

DESCRIPTION Shell transversely subelliptical or suboval, the specimen selected as the holotype being more elongate than the topotype and also a little more inflated, although the latter character may be due to crushing Umbos small, not prominent, situated a little posterior to the middle line Antero-dorsal margin moderately long to long, gently convex to almost straight, gently descendent Anterior end rounded to narrowly rounded Ventral margin long, horizontal, gently convex to almost straight Posterior end a little broken in both specimens, apparently rather rounded as is usual in the genus Postero-dorsal margin similar in disposition to the antero-dorsal margin, but a little shorter The holotype shows moderately widely spaced oblique threads on the anterior part of the surface, the threads being subparallel to the postero-dorsal margin for the larger part of their course, curving round regularly on the upper portion of the shell to slope slightly towards the umbo at the dorsal margin, they are about 0 75 mm apart anteriorly and about 1 1 mm apart on the central portion of the surface The holotype has the ventral margin a little emarginate medially, but this is probably a fortuitous feature as there is no trace of it on the topotype

Dimensions Holotype length 28 0 mm (incomplete), height 13 2 mm Topotype length 21 5 mm (a little incomplete), height 13 1 mm

Remarks The spacing of the oblique threads appears to be characteristic They are distinctly more widely spaced than in *Solecurtus deshayesi* Desmoulins as figured by de Gregorio (1894*a*, p 19, Pl 2, fig 56), from the ?Priabonian of Bassano, as figured by Cossmann & Pissarro (1904*a*, Pl 2, fig 14–1), from the Bartonian of Parnes and from the Lutetian, and than in *Solenocurtus deshayesi* Desmoulins as figured by Cossmann (1906, p 242, Pl 19, figs 26, 27), from the Eocene of Bois-Gouet Compared with *Psammosolen philippii* Speyer (1866, p 31, Pl 4, figs 4, 5), from the Upper Oligocene of Furstenthum Lippe-Detmold, the oblique threads are at quite a different angle, more wide-spaced, and without the V-shaped bend in their course The oblique threads are more closely spaced and more oblique than in *Solecurtus similis* von Koenen (1894, p 1294, Pl 93, figs 8, 9), from the Lower Oligocene of Lattorf In *S parisiensis* Deshayes as figured by Dixon (1850, p 88, Pl 2, fig 24), from the Eocene of Bracklesham, the oblique threads are less widely spaced, and have a V-shaped bend posteriorly

Genus *AZORINUS* Recluz, 1869

(*Act Soc Linn Bordeaux*, **27**, 67)

Type species *Solecurtus coarctatus* Gmelin, Recent = *Solen chamasolen* Da Costa, monotypy

Synonyms *Azor* Leach, in T Brown, 1844 (*Ill Rec Conch Gr Brit and Ir* 2nd ed, p 113) *non* Leach, in Sowerby, 1824 (Moll), type species *Azor antiquatus* (Donovan), Recent, monotypy

Zozia Winckworth, 1930 (*Proc Malac Soc Lond* **19**, 15), type species *Zozia chamasolen* (Da Costa), Recent = *Solen antiquatus* Donovan, original designation

Subgenus *ZOZIELLA* n subg

Type species *Azorinus* (*Zoziella*) *punjabensis* n sp, Lower Eocene

Subgeneric characters Like *Azorinus*, but with strong concentric folds as in *Blagraveia* or *Clementia*

AZORINUS (*ZOZIELLA*) *PUNJABENSIS* n sp

(Figure 85, plate 14)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1844, the holotype, Reg No L 80358, FB F 1850, *1*, FB F 1860, *1*), Green and Nodular Shales (local zone 5) (FB F 1873, *2*)

Description Shell transversely subelliptical, posterior end truncated, little inflated Umbos broken, but they were apparently rather small, moderately distinct and prominent, submedian in position Antero-dorsal margin moderately long, very slightly convex, gently descendent Anterior end rather narrowly rounded. Ventral margin rather long, straight, horizontal except where it merges with the posterior end Posterior end practically vertical, truncated, almost straight, meeting the postero-dorsal margin in a rounded obtuse angle and the ventral margin in a still more rounded but slightly less obtuse angle Postero-dorsal margin rather long, straight, gently descendent Two vague median folds, placed fairly close together (the distance between them being about one and a half times their own width) radiate from the umbo to the middle of the ventral margin, they are fairly straight and vertical, but are slightly concave on their posterior side There are also coarse, rounded concentric folds, of the type found in *Blagraveia* or *Clementia*, covering the whole surface, they are of about the same width as their intervals, and number about 3 in 1 1 mm

DIMENSIONS Holotype length 9 1 mm , height 4 5 mm

REMARKS The writer has not seen any specimens or illustrations of any comparable form, the combination of the two radial folds, such as is found in *Azorinus*, *Solecurtus*, and other related genera, and the coarse concentric folds being apparently unique

Order DESMODONTA

Superfamily MYACEA

Family CORBULIDAE

Genus *CORBULA* Bruguière, 1797

(*Encycl Méth* (*Tabl Vers*), Pl 230)

TYPE SPECIES *Corbula sulcata* Lamarck, Recent, Gray, 1847

SYNONYMS *Aloidis* Mégerle von Muhlfeld, 1811 (*Ges Nat Fr Berlin*, Mag 5, no 1, p 67), type species *A guineensis* Mégerle von Muhlfeld, Recent = *Corbula sulcata* Lamarck, monotypy

?*Harlea* Gray, 1842 (*Syn Cont Br Mus* 44th ed pp 78, 91) (*nomen nudum*)

?*Raleta* Gray, 1842 (*Syn Cont Br Mus* 44th ed pp 78, 91) (*nomen nudum*)

?*Tomala* Gray, 1842 (*Syn Cont Br Mus* 44th ed pp 78, 91) (*nomen nudum*)

REMARKS The above synonymy is based on the assumption that Bruguière's description of the genus in 1792, combined with his unnamed illustrations in 1797, are sufficient to establish the genus There is no doubt at all as to the identity of most of the specimens he illustrated The writer understands that the International Rules of Zoological Nomenclature are intended to validate such cases, and consequently the interpretation of the genus *Corbula* depends upon the first valid designation of a type for *Corbula* Bruguière Schmidt's 1818 type designation for *Corbula* is invalid as three species are given Anton's (1939) type designation for *Corbula* is also invalid as two types are given, one under group '*a*' and one under group '*b*' Children's (1822) type designation is also invalid, since (*a*) it refers to *Corbula* Lamarck, (*b*) *Corbula* Lamarck was not the same as *Corbula* Bruguière, as additional forms were included, and (*c*) a point frequently overlooked is that Children actually gave two types With regard to the latter point, Children in 1822 (*Quart J Lit*, *Sci*, *and Arts* (*R Inst*), **15**, 301) stated '*Corbula* Type *Corbula nucleus* (*Mya inequivalvis* Montag)' and in his footnote ‡ to the word '*nucleus*' 'A kernel Lamarck's sixth species—his type is *C australis*' This is a further reason for invalidating Children's type designation The first valid type designation that the writer can find for *Corbula* Bruguière is that of Gray in 1847 who designated *Corbula sulcata* Lamarck as the type of *Corbula* Bruguière, 1792 It is obvious that *Corbula* Bruguière, 1792 and *Corbula* Bruguière, 1797 are to be treated together, and that they were intended to refer and did refer to the same thing Consequently, the name *Corbula* is here retained for the *C sulcata* group

CORBULA PAKISTANICA n sp

(Figures 124*a*,*b*, plate 17)

Material *Rakhi Nala section* Rubbly Limestones (local zone 6) (FB F 1915, the holotype, Reg No L 80359, and 2 topotypes, Reg No L 80360–1)

Description Left valve transversely oval-subtriangular, strongly inflated and sharply carinated Umbo small, not prominent, rather obtuse, prosogyrous, situated anterior to the middle line at about two-fifths of the length Antero-dorsal margin of moderate length only, apparently only slightly convex, gently descendent Anterior end narrowly rounded Ventral margin gently to moderately convex, meeting the posterior end in a sharply rounded angle which is actually a little more than 90° Posterior end obliquely truncated, of moderate length, straight, sloping upwards distinctly towards the umbo, meeting the postero-dorsal margin in a sharp, obtuse angle Postero-dorsal margin not very long, straight, gently descendent Surface with a sharp carination extending from the umbo to the postero-ventral corner, the portion of the shell posterior to it being distinctly depressed and in a different plane Ornament consisting of rather sharp, distinct, concentric folds which are about half as wide as their intervals, and which are spaced $\frac{1}{2}$ to $\frac{3}{4}$ mm apart These folds persist over the carination on to the posterior area, but they become obsolete on the posterior half of the area

Dimensions Holotype length 10 5 mm height 7 1 mm , thickness (one valve only) 3 2 mm

Remarks The specimens are all left valves *Corbula taramellii* Vinassa de Regny (1896*b*, p 195, Pl 4, figs 2*a*,*b*), from the Chattian of Italy, is more elongate and has distinctly more closely spaced ornament *C aulacophora* Morlet as figured by Boussac (1911*b*, p 45, Pl 10, fig 19), from the Bartonian of Biarritz, and as figured by Cossmann & Pissarro (1904*a*, Pl 3, figs 20–23), is more elongate, has a smaller posterior area, and the ornament is not so coarse *C aulacophora* Morlet race *alpina* Boussac (1911*a*, p 239, Pl 14, fig 32, Pl 15, figs 32, *a*), from the Priabonian of Puget-Theniers and Allons, has a more angular keel and a smaller posterior area *C costata* Sowerby as figured by Cossmann (1921*a*, p 21, Pl 1, figs 43–46), from the Auversian of Biarritz, is more pointed posteriorly, the same species, as figured by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–16), from the Bartonian of Marines, has more closely spaced concentric folds *C grateloupi* Benoist as figured by Cossmann (1921*a*, p 21, Pl 1, figs 47–58), from the Stampian of Gaas, etc , does not have such coarse concentric ornament

CORBULA RAKHIENSIS n sp

(Figures 86*a*,*b*, plate 14)

Material *Rakhi Nala section* Upper Chocolate Clays (upper part, local zone 13) (FB F 1986, the holotype, Reg No L 80362, and 52 topotypes, Reg No L 80363–8, FB F 1995, *10*+, FB F 1996, *10*+), *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F. 2539, *6*, FB F 2536, *6*, FB F 2521, *2*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2738, *2*)

Description Shell uniformly of small size, only a little more than 2 mm long, corbuliform, subtriangular in outline, rather strongly inflated, right valve a little larger than the left valve but not very much so Umbos small, pointed, prominent, incurved, slightly prosogyrous, situated anterior to the middle line at about one-third of the length Antero-dorsal margin of moderate length, about the same length as the postero-dorsal margin, very slightly convex, steeply descendent Anterior end moderately narrowly rounded Ventral margin moderately convex Posterior end truncated, short, vertical, almost straight, very slightly convex, meeting the postero-dorsal margin in a broad, gently rounded, obtuse angle, and the ventral margin in a more abrupt, but still rounded angle Postero-dorsal margin almost straight, slightly convex, moderately steeply descendent, but considerably less steep than the antero-dorsal margin Umbonal slope on right valve well defined but not carinate Umbonal slope on left valve more strongly marked, separating off a depressed posterior area The holotype shows traces of the ornament, both valves being ornamented with rather fine, closely spaced concentric folds or threads the intervals between which appear to have been narrower than the threads themselves, there seem to have been about 14 or 15 threads in ¾ mm on the central portion of both valves The left valve of a topotype, however, shows that coarse folds (6 or 7 in ¾ mm), with intervals at least as wide as the ribs, are present ventrally

There is a small amount of variation in the degree of elongation (one specimen has a length of 1 5 mm and a height of 1 1 mm), but the general characters remain constant

Dimensions Holotype length 2 2 mm , height 1 9 mm , thickness (both valves) 1 4 mm

Remarks The specimens are all moulds *Corbula chmeietensis* Oppenheim (1906*a*, p 198, Pl 19, fig 5), from the Upper Mokattam of Egypt, is not so high and is still smaller *C dactylus* Oppenheim (1915, p 35, Pl 2, figs 12, 13), from the Eocene of Togo, is larger and more elongate *C obovata* von Koenen (1894, p 1300, Pl 92, figs 1–3), from the Lower Oligocene of northern Germany, is smaller and distinctly more rostrate *C* (*Agina*) *pisum* Sowerby as figured by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–6), from the Bartonian of Le Ruel, has more swollen umbos, is more inequivalve, is larger, and appears to belong to the subgenus *Varicorbula*

CORBULA SORIENSIS n sp

(Figures 87*a*,*b*,*c*, plate 14)

Material *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2564, *6*, FB F. 2562, the holotype, Reg No L 80369, and 1 topotype, Reg No L 80370, FB F 2561, *11*, Reg No L 80610–6)

Description Shell of moderately small size, fairly robust, corbuliform, subtriangular to oval-subtriangular depending upon the state of preservation, with a tendency to being cuneiform posteriorly in well-preserved specimens, the right valve a little larger than the left valve, but not markedly so Umbos small, prominent or moderately prominent, distinct, incurved and slightly prosogyrous Antero-dorsal margin of moderate length, steeply or moderately steeply descendent, gently convex Anterior end rounded or moderately narrowly rounded, situated low down Ventral margin gently convex Posterior end in well-preserved specimens with a short, blunt rostrum which is situated low down and is subrectangular in outline, in most of the specimens this feature is not observed, the posterior outline being more normally corbuliform Specimens of the latter type show a superficial resemblance to *Corbula rakhiensis* n sp , but they are usually more transverse, have considerably coarser ornament, and are larger Postero-dorsal margin of moderate length, straight, and steeply to moderately steeply descendent Umbonal slope on right valve vague to moderately distinct, but not carinate, marked by an angular or subangular change in direction of the concentric ornament Umbonal slope of left valve similar, but tending to be more marked, the posterior area thus separated off being more distinct and more excavated than on the right valve Ornament of right valve consisting of concentric folds which are finer and more widely spaced medially than ventrally, varying from 7 to 4 in ¼ mm , in the central portion of the surface the intervals may be as much as one and a half to two times as wide as the folds or threads, while ventrally, where the folds are coarser, the intervals are never wider than the folds Ornament on left valve relatively finer and more widely spaced, consisting of rather sharp concentric threads whose intervals are at least twice as wide as the threads, and which are about 7 to 5 to ¼ mm in number

Dimensions Holotype length 3 75 mm , height 2 75 mm , thickness (both valves) 2 0 mm

Remarks The distinction from *Corbula rakhiensis* has been mentioned above *C subaequivalvis* Sandberger as figured by Kissling (1896, p 47, Pl 4, figs 12*a*,*b*, 13), from the Middle Oligocene of Courgenay and Bressaucourt (Berner Jura), is somewhat similar in shape, but is larger, more elongate, and apparently smooth *C soriensis* is definitely ornamented, and although the umbonal region in the specimens recorded appears to be smooth, this may be due to abrasion The shell does not seem to be sufficiently inequivalve or the ornament of the two valves sufficiently distinct for the subgenus *Varicorbula*

CORBULA PUNJABENSIS n sp

(Figures 88*a*,*b*,*c*, plate 14)

Material *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 80371)

Description Shell of moderate size, distinctly triangular in outline, distinctly wider than high, moderately inflated, only slightly inequivalve, the right valve being slightly larger than the left valve Umbos prominent, not broad, submedian in position Antero-dorsal margin moderately long, moderately to moderately steeply descendent, only slightly convex Anterior end rather narrowly rounded, situated distinctly low down Ventral margin long, subhorizontal, only slightly convex Posterior end obliquely truncated, straight, not very short, sloping upwards rather obliquely towards the umbos, forming a fairly sharp, acute angle of a little less than 90° with the ventral margin, and joining the postero-dorsal margin in a rounded, obtuse angle Postero-dorsal margin rather short, fairly straight, moderately descendent Umbonal slope quite distinct but not carinated, separating off a rather small, depressed posterior area Ornament on the two valves almost identical, consisting of fine concentric threads of about the same width as their intervals, they are a little finer on the right valve (7 in ¼ mm) than on the left valve (5 in ¼ mm)

Dimensions Holotype· length 8 6 mm , height 5 8 mm , thickness (both valves) 4 3 mm

Remarks *Corbula samanaensis* Cox (1930*a*, p 211, Pl 22, figs 14, 15*a–c*), from the Hangu Shales of Hangu and from Bed 11 of the Ranikot at Fort Lockhart in the Samana Range, has a much more convex ventral margin, especially in its anterior part, the postero-ventral corner is situated higher up, and the umbos are also broader *C chmeustensis* Oppenheim (1906*a*, p 198, Pl 19, figs 5*a*,*b*), from the Upper Mokattam of Egypt, is less elongate *C striatina* Deshayes (1857, p 222, Pl 12, figs 12–17), from the Lower Sands of Mercin, Cuise-la-Motte, Laversine, Cuisy-en-Almont, Bantelu, Laon, and the Vivray valley, is less triangular, with a more convex ventral margin, and is less transverse, the same species as figured by Netschaew (1897, p 119, Pl 8, fig 5), from the Eocene of the Volga region, and by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–13), from the Cuisian of Cuise, appears to be less inflated *C nicensis* Bellardi as figured by Boussac (1911*a*, p 237, Pl 16, figs 21–26), from the Auversian of La Palarea, is less transverse *C pixidula* Deshayes (1857, p 223, Pl 12, figs 18–23), from the Calcaire Grossier and Middle Sands of Parnes, Monneville, Chery-Chartreuve, Auvers, and Mary, and from La Palarea, is more obliquely truncated and more pointed posteriorly, less triangular, and has less median umbos, the same differences apply to illustrations of the species by Doncieux (1911, p 124, Pl 15, figs 4, 5), from the Middle Lutetian of Coustouge, by Cossmann (1906, p 234, Pl 18, figs 20, 21), from the Eocene of Bois-Gouet, Coislin, and Arthon, and by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–14), from the Bartonian of Chery-Chartreuve and from the Cuisian and Lutetian

CORBULA PSEUDORAKHIENSIS n sp

(Figures 89*a*,*b*,*c*, plate 14)

Material *Zinda Pir section* Ghazij Shales (local subzone 3*b*) (FB F 2678, the holotype, Reg No L 80372, and 11 topotypes, Reg No L 80373–8, FB F 2677,*2*, FB F 2676,*1*)

Description Shell of small size, subtriangular to oval-subquadrate in outline, somewhat truncated posteriorly, moderately strongly inflated, slightly inequivalve, the right valve being slightly the larger Umbos prominent and pointed, slightly prosogyrous, submedian in position Antero-dorsal margin of moderate length only, almost straight, very slightly convex, moderately steeply descendent Anterior end moderately narrowly rounded, situated fairly low down Ventral margin gently convex Posterior end subtruncated, rather short, subvertical as a whole, gently but distinctly convex, meeting the ventral margin in a rounded angle of a little more than a right angle, merging insensibly into the postero-dorsal margin in a well-rounded curve Postero-dorsal margin of moderate length only, slightly convex, moderately to moderately steeply descendent Umbonal slope on left valve marked by a blunt but distinct carina separating off a gently excavated posterior area Umbonal slope of right valve similarly defined Umbonal region of valves often appearing smooth, probably due to abrasion Left valve ornamented with relatively coarse concentric folds of about the same width as their intervals, there being about 5 or 6 in ½ mm Ornament of right valve somewhat similar, but more often undeveloped or abraded, it appears to be a little less coarse

Dimensions Holotype length 2 1 mm , height 1·6 mm , thickness (both valves) 1 25 mm

REMARKS *Corbula rakhiensis* n sp has more projecting umbos and is less transverse *C soriensis* n sp is distinctly and uniformly larger, more transverse, and has coarser ornament *C chmeietensis* Oppenheim (1906*a*, p 198, Pl 19, figs 5*a*,*b*), from the Upper Mokattam of Egypt, is less trapezoidal in outline, and is equivalve *C nicensis* Bellardi as figured by Boussac (1911*a*, p 237, Pl 16, figs 21–26), from the Auversian of La Palarea, is usually not so high, and the umbos are more exactly median in position *C pixidula* Deshayes (1857, p 223, Pl 12, figs 18–23), from the Calcaire Grossier and Middle Sands of Parnes, Monneville, Chery-Chartreuve, Auvers, and Mary, and from La Palarea is distinctly larger, more transverse, and differently ornamented, the same differences apply to illustrations of this species by Doncieux (1911, p 124, Pl 15, figs 4, 5), from the Middle Lutetian of Coustouge, and by Cossmann (1906, p 234, Pl 18, figs 20, 21), from the Eocene of Bois-Gouet, and Arthon *C striatina* Deshayes as figured by Netschaew (1897, p 119, Pl 8, fig 5), from the Eocene of the Volga region, and by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–13), from the Cuisian of Cuise, is more elongate *Corbula* (*Agina*) cf *minuta* Deshayes as figured by Cossmann (1906, p 234, Pl 18, figs 14, 15), from the Eocene of Bois-Gouet, and *C* (*Agina*) *minuta* Deshayes as figured by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–10), from the Lutetian of Villiers and from the Bartonian, is a little less triangular and more trapezoidal, the posterior truncation being less steep, and the posterior margin longer

CORBULA sp A

(Figure 125, plate 17)

MATERIAL *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 14) (FB F 2517, the holotype, Reg No L 80379)

DESCRIPTION Shell subtriangular in outline, not very high, and with a submedian umbo which is apparently rather broad Valve not seeming to have been strongly inflated, but this appearance of moderate inflation may be due to the fact that it is preserved on a shale surface and has been somewhat compressed Antero-dorsal margin moderately long, slightly convex, moderately steeply descendent Anterior end narrowly rounded, situated rather low down Ventral margin gently convex Posterior end rostrate, bluntly pointed, situated very low down Postero-dorsal margin very similar to the antero-dorsal margin but less convex, being straight in its median and distal portions Ornament consisting of moderately coarse concentric folds which increase slowly and regularly in size and of about the same width as their intervals, there are 4 in $\frac{3}{4}$ mm

DIMENSIONS Holotype length 8 25 mm , height 5 25 mm

REMARKS The solitary specimen is a poorly preserved left valve the characters of which do not seem to agree with those of any of the known species from India or Pakistan, or with any of the species here described *Corbula cercus* Oppenheim (1904, p 269, Pl 7, figs 4, 5), from the Eocene of the Cameroons, is less elevated

Subgenus *VARICORBULA* Grant & Gale, 1931

(*Mem San Diego Soc nat Hist* 1, 12, 420)

TYPE SPECIES *Corbula* (*Varicorbula*) *gibba* (Olivi), Miocene-Recent, original designation

SYNONYM '*Agina* Turton' *auct non* Turton

Remarks *Notocorbula* Iredale, 1930 (*Rec Austral Mus* **17**, 404—type species· *N vicaria* Iredale, Recent, original designation) is very similar to *Varicorbula*, but the left valve has some radial ornament Should the two forms eventually prove to be synonymous, the following forms referred to the subgenus *Varicorbula* would be referred to the subgenus *Notocorbula*

CORBULA (*VARICORBULA*) *HARPA* d'Archiac & Haime, 1854

References *Corbula harpa* d'Archiac & Haime, 1854 (pp 236, 359, 365, Pl 16, figs 8, *a*, *b*, 9), Blanford, 1878 (p 165), Medlicott & Blanford, 1879*b* (pars) (pp 449, 453), Duncan, 1880 (pp 5, 8), Blanford, 1880 (pp 35, 40, 40–41), Fedden, 1880 (p 201), Zittel, 1883 (p 93), Waagen, 1886 (p 24), R D Oldham, 1893 (p 288), Noetling, 1897 (p 53), Noetling, 1901 (p 246), Douvillé, 1928 (p 1), Vredenburg, 1928*a* (p 6), Douvillé, 1929 (p 27), Cox, 1930*a* (pp 213, 141)

C harpa d'Archiac, Oppenheim, 1901*a* (p 308)

C (*Agina*) *harpa* d'Archiac & Haime, Cossmann & Pissarro, 1927 (pp 28, 4, Pl 1, fig 23, Pl 4, figs 26–32), Douville, 1929 (p 67), Checchia-Rispoli, 1935 (p 45, Pl 1, figs 4, 5)

Agina harpa (d'Archiac & Haime), Douvillé, 1929 (p 72)

Argina harpa (d'Archiac & Haime), Douvillé, 1929 (Pl 10, figs 39–44)

Corbula (*Agina*) *harpa* d'Archiac & Haime, var *trigona* Douvillé, 1929 (p 68 = figs 40–44)

C (*Agina*) *harpa* d'Archiac & Haime, mut *brevis* Douvillé, 1929 (p 68 = fig 39)

Doubtful references *Corbula harpa* d'Archiac & Haime, Garde, 1911 (p 93), Oppenheim, 1915 (p 89), Douvillé, 1920*b* (pp 156, 158)

C harpa Forbes, Douvillé, 1920*a* (p 113)

Material *Rakhi Nala section Venericardia* Shales (local zone 1) (FB F 1836, *4*, Reg No L 80380–3)

Further distribution in Pakistan *Cardita beaumonti* Beds of Choya Saidan Shah, the anticline west of Ranikot, the Barki Nala (on road to Laki Lak within outer ridge of limestone), hills north of Ranikot (east of range), and low ground below Jakhmari scarp, Upper Ranikot (zone 1) of Western Pakistan, Upper Ranikot (zone 2) of Western Pakistan, Upper Ranikot (zone 3) of the Ghari-wari Gorge section (on road from Badha to Leilan old coal-pit), Upper Ranikot (zone 4) of Jherruck, and north-west of Kotri The type locality is in the 'Hala Range' The type localities for the 'variety' *trigona* and the 'mutation' *brevis* are in the *Cardita beaumonti* beds west of Ranikot

Further distribution Maestrichtian of Tripolitania The doubtful records given above refer to occurrences in the Eocene of the Soudan, there have been several misidentifications of fossils from these beds, and since specimens of the species from the Soudan have not been illustrated, the records should remain doubtful pending a re-examination

CORBULA (*VARICORBULA*) *PSEUDOPISUM* n sp

(Figure 90, plate 14)

Material *Rakhi Nala section Pellatispira* Beds (local zone 15) (FB F 1997, *2*, FB F 1992, *10+*, FB F 1993, the holotype, Reg No L 80384, and 19 topotypes, Reg No L 80385–90), *Zinda Pir section*· Upper Chocolate Clays (upper part, local zone 13) (FB. F. 2519, *10+*), *Pellatispira* Beds (local zone 15) (FB F 2503, *2*, FB F 2502, *2*)

DESCRIPTION Shell small, corbuliform, right valve larger than the left and more strongly ornamented Right valve rather high, with prominent, apparently rather broad umbos which are submedian or slightly anterior to the median line in position, orbicular-subquadrate in outline, probably more inflated than the left valve Antero-dorsal and postero-dorsal margins steeply descendent Anterior end moderately sharply rounded, situated rather low down Ventral margin regularly and rather strongly convex. Posterior end truncated, moderately long, slightly convex, sloping upwards gently towards the umbos, meeting the ventral margin in a bluntly rounded angle of a little more than a right angle Ornament consisting of strong, broad, raised concentric folds or ribbons of about the same width as their intervals (3 in ¾ mm ventrally), these folds form a small V-shaped angulation (the apex of the V directed towards the postero-ventral corner) where they cross the rather angular carination extending from the umbo to the postero-ventral corner Ornament on the area posterior to the carination obsolete Only one left valve and its impression is preserved, it is less high and more transverse, with smaller and less projecting umbo, transversely oval-subtriangular in outline, a little produced and narrower posteriorly Ornament not preserved, but obviously not of the strong type found on the right valve

DIMENSIONS Holotype length 4 0 mm , height 3 75 mm (a little incomplete) Topotype (left valve) length 3 25 mm , height 2 4 mm

REMARKS The specimens are all somewhat crushed, none retaining their natural degree of inflation The species is smaller, has flatter concentric folds, the ornament is not so fine umbonally, and the outline is more quadrate than in *Corbula* (*Varicorbula*) *prototruncata* Noetling from the Oligocene and Miocene of Burma It is more transverse and the intervals between the concentric folds are rather wider than in *C* *gibba* Olivi as figured by Speyer (1884, Pl 2, figs 4–7), from the Chattian of Cassel The ventral margin is less obliquely bulging, the posterior area more sharply defined by the keel, and the concentric folds bend down slightly towards the keel, compared with *C* (*Agina*) *pisum* Sowerby as figured by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–6), from the Bartonian of Le Ruel It is higher than *C* (*Agina*) *subpisum* d'Orbigny as figured by Cossmann (1921*a*, p 25, Pl 1, figs 81, 82), from the Stampian of Lesbarritz and Caudéran, and higher and with coarser ornament than *C* *subpisum* d'Orbigny as figured by Deshayes (1857, p 216, Pl 12, figs 24–28), from the Fontainebleau Upper Sands of France, Switzerland, Germany, and Belgium

CORBULA (*VARICORBULA*) *PSEUDOCICER* n sp

(Figures 126*a*, *b*, *c*, *d*, plate 17)

MATERIAL *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 13) (FB F 2519, the holotype, Reg No L 80391), *Pellatispira* Beds (local zone 15) (FB F 2502, 3, Reg No L 80392–4)

DESCRIPTION Shell of moderate size, strongly inflated, corbuliform, subtriangular-cuneiform, rather produced posteriorly Right valve a little larger, with much stronger ornament Umbo broad, not very prominent on account of being incurved, situated a little anterior to the middle line at about two-fifths of the length Antero-dorsal margin of moderate length, slightly convex, moderately steeply descendent Anterior end rather narrowly rounded Ventral margin regularly and moderately convex, slightly emarginate posteriorly where it rises fairly sharply to the posterior end Posterior end bluntly rostrate, truncated, more or less straight, very short, rising upwards obliquely a little towards the umbo, joining the adjacent margins in rounded, obtuse angles Postero-dorsal margin moderately long, slightly concave, only gently descendent Surface with a fine, sharp carina in the umbonal region travelling towards the postero-ventral corner, near which it becomes a bluntly rounded angulation Ornament in the young stage consisting of fine concentric threads (about 7 in ¾ mm) with irregular intervals (once to twice as wide as the threads), these give rise to coarse concentric folds on the adult shell, the folds being rounded and of about the same width as their intervals, and only 3 in ¾ mm in spacing Folds finer and tending to become scaly all over the posterior area Right valve more triangular, very strongly inflated along a line from the umbo to the antero-ventral corner, and more finely ornamented Umbo prominent, submedian Antero-dorsal margin moderately long, rather steeply descendent Anterior end narrowly rounded Ventral margin gently convex Posterior end rostrate, pointed, situated low down Postero-dorsal margin moderately long, fairly straight, rather steeply descendent A fine carination, becoming rather blunt in the adult portion of the shell, runs from the umbo to the posterior pointed end Ornament consisting of fine, low but sharp, rather widely spaced, concentric threads (5 or 6 in ¾ mm in the central portion of the valve), which tend to become obsolete ventrally

DIMENSIONS Holotype height at least 4 9 mm , thickness (both valves) 4 0 mm , dimensions measured along growth lines of right valve length 5 6 mm , height 3 75 mm

REMARKS *Corbula acer* Vinassa de Regny as figured by Boussac (1911*a*, p 239, Pl 16, figs 44, *a*, 47, 48), from the Priabonian of Puget-Théniers and Allons, and from the Auversian of Puget-Théniers, is larger, has less accentuated ornament on the right valve, the ornament of the left valve not becoming obsolete, and the right valve umbo not quite so broad *C lamarcki* Deshayes as figured by Glibert (1933, p 162, Pl 10, fig 8), from the Bruxellian of Neder-Ockerzeel (Belgium), and as figured by Cossmann & Pissarro (1904*a*, Pl 3, fig 20–12), from the Lutetian of Ferme de l'Orme and from the Bartonian, has the ornament of the right valve less coarse ventrally, and its left valve is more transverse and less triangular *C nicensis* Bellardi as figured by Boussac (1911*a*, p 237, Pl 16, figs 21–26), from the Auversian of La Palarea, is a little larger, less cuneiform, has less prominent umbos, and its left valve has less closely spaced concentric ornament, which does not tend to become obsolete ventrally *C valdensis* Hébert & Renévier as figured by Boussac (1911*a*, p 238, Pl 15, figs 30, *a*, 42, *a*, Pl 16, figs 27, *a*, 46, *a*), from the Bartonian (Lower Priabonian) of La Cordaz, is less cuneiform, a little larger, the ornament on the right valve does not become so coarse, and the ornament of the left valve does not tend to become obsolete *C cercus* Oppenheim (1904, p 269, Pl 7, figs 4, 5), from the Eocene of the Cameroons, is not so high

Subgenus *BICORBULA* Fischer, 1887

(*Man Conch* p 1123)

TYPE SPECIES *Corbula gallica* Lamarck, Eocene, monotypy

CORBULA (*BICORBULA*) *SUBEXARATA* d'Archiac & Haime, 1854

REFERENCES *Corbula subexarata* d'Archiac, 1850*b* (*nomen nudum*) (3, 258), d'Archiac & Haime, 1854 (pp. 235, 365, Pl 16, figs. 10, *a*, 11), Ball, 1874 (p 152), Medlicott & Blanford, 1879*b* (pp 459, 531), Duncan, 1880 (p 9), Blanford, 1880 (pp 48, 119, 127), Fedden, 1880 (p 201), Cotter, 1912 (pp 224, 226, 234), L M Davies, 1925 (p 213), L M Davies, 1926*b* (p 200), Cotter, in Cossmann & Pissarro, 1927 (p 4), Douvillé, 1928 (p 22), Cox, 1930*a* (p 213), Cotter, 1938 (p 70), Clegg, 1938 (pp 205, 206, 208, 209, 253), Furon, 1941 (p 335), Rossi, 1942 (pp 116, 122), Krishnan, 1943 (p 447)

Thracia costata Bellardi, 1854 (p 17, Pl 2, fig 6, *non C costata* Brown, 1845–9 *nec* Sowerby, 1850)

Corbula harpaeformis Oppenheim, 1906*a* (p 193, Pl 18, figs 7–10), Klebelsberg, 1913 (pp 375, 378), Cuvillier, 1930 (pp 171, 275, etc)

C (*Bicorbula*) *ickei* Martin, 1915 (p 190, Pl 8, figs 209, 209*a–c*, 210, 211), Martin, 1931 (p 46, Pl 7, fig 2)

C subexarata d'Archiac var *lituus* Cotter, 1923 (p 6 (pars), Pl 1, figs 2–5), Cotter, 1938 (p 68)

C (*Bicorbula*) *subexarata* d'Archiac, Cotter, 1923 (p 3), Cox, 1931*a* (pp 84, 28, 29, 33, 34, Pl 4, figs 14*a*,*b*), Brown, 1931 (p 267), Cotter, 1933 (p 98), Chhibber, 1934 (p 226), Cox, 1936 (pp 33, 7, Pl 4, figs 4, 5), Rossi, 1942 (p 182, Pl 10, figs 12*a–d*)

C ickei Martin, Van der Vlerk, 1931 (p 283)

C (*Bicorbula*) *subexarata* d'Archiac & Haime var *lituus* Cotter, Brown, 1931 (p 267)

Corbula cf *harpaeformis* Oppenheim, Cuvillier, 1933 (p 25, Pl 3, figs 10, 11, 16)

Corbula n sp Rossi, 1942 (p 183, Pl 10, fig 13)

MATERIAL *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F 1842, *2*, FB F 2015, *2*, FB F 1843, *10+*, FB F 1844, *1*, FB F 1845, *2*, FB F 1848, *2*, FB F 1849, *1*, FB F 1852, *1*, FB F 1853, *2*, FB F 1854, *10+*, FB F 2022, *1*, FB F 1855, *1*, FB F 1856, *1*), Green and Nodular Shales (local zone 6) (FB F 1897, *4*, FB F 1899, *1*, FB F 1900, *6*, FB F 1901, *1*, FB F 1902, *1*, FB F 1903, *2*), Rubbly Limestones (local zone 6) (FB F 1910, *2*, FB F 1911, *1*, FB F 1912, *6*, FB F 1915, *1*, FB F 1916, *2*), Shales with Alabaster (local zone 7) (FB F 1930, *2*, FB F 1931, *2*, FB F 1932, *2*, FB F 1935, *10+*, FB F 1943, *6*, FB F 1944, *1*, FB F 1948, *2*), Lower Chocolate Clays (local zone 10) (FB F 1966, *2*, FB F 1967, *2*, one of which is large and very well preserved, Reg No L 80395–6) *Zinda Pir section* Zinda Pir Limestones (lower part, local zone 1) (FB F 2687, *6*), Ghazij Shales (local subzone 3*a*) (FB F 2679, *1*), Ghazij Shales (local subzone 3*b*) (FB F 2677, *2*, FB F 2676, *10+*, FB F 2675, *10+*), Lower Chocolate Clays (local zone 10) (FB F 2571, *2*, FB F 2558, *1*, FB F 2733, *1*, FB F 2567, *1*, FB F 2554, *2*, FB F 2551, *1*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2541, *1*, FB F 2539, *2*, FB F 2537, *1*, FB F 2522, *6*), Upper Chocolate Clays (upper part, local zone 13) (FB F 2520, *2*), Upper Chocolate Clays (upper part, local zone *14*) (FB F 2517, *2*, FB F 2516, *2*), *Kohat area* (*Tarkhobi section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2164, *1*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2173, *2*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *1*), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *1*, FB F 2291, *1*), Kaladhand Limestone (local subzone 4*a*) (FB F 2245, *4*, FB F 2255, *15+*, FB F 2295, *3*), Upper Kohat Shales (local subzone 4*a*) (FB F 2256, *1*, FB F 2257, *2*), *Kohat area* (*Shekhan Nala section*) Lower Kohat Shales (local subzone 4*a*) (FB F 2332, *1*), Kaladhand Limestone (local subzone 4*a*) (FB F 2335, *3*, FB F 2336, *1*), Upper Kohat Shales (local subzone 4*a*) (FB F 2337, *2*, FB F 2338, *1*, FB F 2341, *1*, FB F 2342, *1*)

Accessory samples· *Kohat area* (*Tarkhobi*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2192, *1*), Middle Shekhan (local zone 3) (FB F 2180, *1*), Kohat Shales (local subzone 4*a*) (FB F 2183, *8*, FB F 2184, *1*)

FURTHER DISTRIBUTION IN PAKISTAN Ghazij Shales near Hindu Bagh, Laki of Sind ('Hala Range'), and Baluchistan, Kohat Shales of Kohat, and Bahadur Khel, Middle Khirthar of the Dera Ghazi Khan District, Khirthar of Malin, the Laki Valley, and Subathu, Eocene of the Luni Pathan Hills The 'Hala Range' is the type locality

FURTHER DISTRIBUTION Lower Mokattam of Egypt, Eocene of Bahrein Island, and Somaliland, Upper Mokattam of Egypt, Upper or Middle Eocene of Sirtica, Yaw Stage of Burma (numerous localities—type area for the 'variety' *lituus*), Upper Eocene of Java (type locality for *ickei*)

REMARKS Cotter's record from the Shwezetaw Stage 1 mile north of Peinhnebin in Burma (1923, p 6) is here omitted, if the identification is correct, the stratigraphical horizon is almost certainly Yaw Stage rather than Shwezetaw Stage, on the other hand, if the stratigraphical horizon is correct, the identification is almost certainly incorrect, and the specimens are probably to be referred to one of the known Burma Lower Oligocene species such as *Corbula* (*Varicorbula*) *prototruncata* Noetling

Superfamily GASTROCHAENACEA

Family GASTROCHAENIDAE

Genus *EUFISTULANA* n nom

TYPE SPECIES *Gastrochaena mumia* Spengler, Recent, here designated

SYNONYM *Fistulana* (Bruguière, 1789, *Encycl Méth* (Vers), **1**, xii, *nomen nudum*) *auct non* Muller, 1776 (Coel)

REMARKS Iredale (1915, pp 296–297), with whom Prashad (1932, p 315) agreed, concluded that the type of *Gastrochaena* Spengler was *G mumia* Spengler, which made the name *Gastrochaena* apply to those forms previously referred to *Fistulana* Bruguière, and left the name *Rocellaria* Blainville, 1828–9 to apply to those forms previously placed in *Gastrochaena* This conclusion was based on the writing of H & A Adams, 1856 (*Gen Rec Moll* **2**, 334–336), which he quoted, and regarded as fixing the type H & A Adams, however, merely gave an example, stated that the species on which Spengler founded the genus was now known under another name, and that this latter species was the type of *Chaena* Retzius Actually, there were three species in Spengler's original list, and only a definite type designation can settle the status of the genus In the writer's opinion, H & A Adams did not designate a type Furthermore, a type was legitimately designated by Children in 1822 (*Quart J Lit*, *Sci and Arts* (*R Inst*), **14**, 83) who cited '*Gastrochaena* Type *Gastrochaena cuneiformis Pholas hians* Chemnitz' His book was a translation of Lamarck, essentially, and on referring to Lamarck (*Hist nat An s Vert* **5**, 446–447) it is seen that he mentions the genus '*Gastrochaena* de Spengler', consequently there is no doubt as to the *Gastrochaena* Children was considering Moreover, Lamarck included *Pholas hians* Chemnitz as a synonym of *Gastrochaena cuneiformis* Spengler, so that there is no doubt that Children only designated one species as the type of *Gastrochaena* Spengler This conclusion means that there is no name for those forms that have been referred to as *Fistulana*, and these forms are accordingly here named *Eufistulana* with *Gastrochaena mumia* Spengler as type

EUFISTULANA ELONGATA (Deshayes), 1824

REFERENCES *Fistulana elongata* Deshayes, 1824 (p 15, Pl 4, figs 17–19), Morton, 1834 (pars) (pp 87, 8), Bronn, 1848*a* (p 375), d'Orbigny, 1850 (p 375), Pictet, 1855 (p 342), Deshayes, 1857 (p 97, Pl 2, fig 11), Mourlon, 1881 (p 191), Frauscher, 1886 (p 240, Pl 11, fig 9, ?*non* Pl 12, fig 8 (var)), Schlosser, 1925*a* (pp 77, 177), Cox, 1931*a* (pp 85, 29, 32, 34, Pl 4, fig 15), Cotter, 1933 (p 98), Heron, 1937 (p 23), Heron, 1938 (p 82), Furon & Soyer, 1947 (pp 51, 87)

Kuphus rectus (J de C Sowerby), Fedden, 1880 (pars) (p 210)

Fistulana elongata Lamarck, Cossmann & Pissarro, 1904*a* (Pl 1, fig 2–1), Cuvillier, 1930 (p 172)

F aegyptiaca Oppenheim, 1906*a* (p 204, Pl 22, fig 35, ?*non* Pl 19, fig 10 = ?*Kuphus* sp)

Fistulana cf *elongata* Deshayes, Cuvillier, 1933 (p 26, Pl 3, figs 15, 15*a*)

MATERIAL *Rakhi Nala section Pellatispira* Beds (local zone 15) (FB F 1980, *1*, Reg No L 80397), *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2540, *1*, FB F 2539, *1*, FB F 2535, *1*), Upper Chocolate Clays (upper part, local zone 14) (FB F 2517, *2*), *Kohat area* (*Sirki Paila*) Sirki Shale/Kohat Limestone (local subzone 4*d*) (FB F 2114, *8*, Reg No L 80398–403)

FURTHER DISTRIBUTION IN PAKISTAN Kohat Shales of Kohat, and Bahadur Khel, Upper Khirthar Shales 1 mile north-east of Nili Kach (south of Gumal), Khirthar of Kund (3 miles south-west of Kotkai), and 1½ miles north-west of Sambaza

FURTHER DISTRIBUTION Ypresian of Egypt, Cuisian of France, Lower Mokattam of Egypt, Lutetian of France, Middle Eocene of the Bavarian Alps, and Somaliland, Upper Mokattam of Egypt

REMARKS The record from the *Pellatispira* Beds of the Rakhi Nala section seems to be the highest known occurrence of the species unless, as does not seem likely, the occurrence in the Upper Mokattam of Egypt is younger

Superfamily ADESMACEA

Family TEREDIDAE

Genus *TEREDO* Linné, 1758

(*Syst Nat* 10th ed p 651)

TYPE SPECIES *Teredo navalis* Linné, Recent, Children, 1822

SYNONYMS *Teredolites* Leymerie, 1841 (*nomen nudum*) (*Mem Soc géol Fr* 4, pt 2, p 341).

Teredolites Leymerie, 1842 (*Mem Soc géol Fr* 5, pt 1, p 2), type species *Teredolites clavatus* Leymerie, Cretaceous, monotypy

Xylophagus (Gronovius, 1781) Herrmannsen, 1847 (*Indicis Gen Malacoz* 2, 713) (= *Teredo*)

Polorthus Gabb, 1861 (*Proc Acad Nat Sci Philad* pp 366, 367), type species if not yet chosen, to be selected from the two Cretaceous species *Teredo tibialis* Morton and *Polorthus americana* (Gabb)

Polorthis auct (error)

TEREDO TOURNALI Leymerie, 1846

REFERENCES *Teredo* sp d'Archiac, 1844 (p 178)

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Septaria tarbelliana d'Archiac, 1846 (p 207, Pl 8, fig 11), d'Archiac, 1850*a* (p 452), Tournouer, 1872*a* (p 500), Mallada, 1883 (Pl 7A, fig 7), Moll, 1942 (p. 141)

Vermetus laevis Bellardi, 1852 (p 228, Pl 15, fig 4)

Teredo thournali Leymerie?, Sismonda, 1852 (p 324)

Septaria? tarbelliana d'Archiac, E Pavay, 1871 (pp 365, 424)

Teredo tournali d'Archiac?, Tournouer, 1872*a* (p 503)

Teredo cf *tournali* Leymerie, Vinassa de Regny, 1896*a* (pp 227, 234)

T intestinoides Cossmann & Pissarro, 1927 (p 30, Pl 2, fig 39, Pl 4, fig 25), Cox, in L M Davies & Pinfold, 1937 (p 8), Moll, 1942 (p 149)

MATERIAL *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 2) (FB F 1835, *1*, Reg No L 80404), Upper Chocolate Clays (upper part, local zone 14) (FB. F 1991, *1*), *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB. F. 2539, *2*), *Kohat area* (*Tarkhobi section*) Tarkhobi Shales (lower part, local zone 1) (FB F 2150, *1*), Lower Shekhan Limestone (local subzone 3*a*) (FB F. 2161, *3*, FB. F 2162, *2*), Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, *2*), *Kohat area* (*Panoba section*) Lower Shekhan

Limestone (local subzone 3*a*) (FB F 2121, *1*, FB F 2292, *1*), Middle Shekhan Limestone (local subzone 3*b*), (FB F 2287, *1*), *Kohat area* (*Shekhan Nala section*) Lower Shekhan Limestone (local subzone 3*a*) (FB F 2377, *1*, FB F 2313, *1*), *Kohat area* (*Gada Khel*) Lower Shekhan Limestone (local subzone 3*a*)(FB F 2102, *2*)

Accessory samples *Kohat area* (*Tarkhobi*) Tarkhobi Shales (25 ft above *Irregularis* Bed› local zone 2) (FB F 2188, *2*), Lower Shekhan Limestone (local subzone 3*a*) (FB. F 2193, *4*, FB F 2196, *1*), Kohat Shales (local subzone 4*a*) (FB F 2184, *4*)

FURTHER DISTRIBUTION IN PAKISTAN Patala Shales of the Salt Range, Upper Ranikot (zone 3) of Jherruck, and 3 miles east of Leilan old coal-pit (Band Vero Plain east), Upper Ranikot (zone 4) of Jherruck, and the left bank of the Indus opposite Jherruck

FURTHER DISTRIBUTION This well-known and common species has a wide distribution and a long geological range, the following is a summary of its distribution Lower Eocene of Egypt, Lower Lutetian of France, Middle Lutetian of France, Lutetian of northern Spain, Asia Minor, the Balkans (north-east Bulgaria), Croatia, Dalmatia, and Venetia, Mokattam of Egypt, Middle Eocene of the Bavarian Alps, Auversian of Venetia, and La Villa Marbella (Biarritz), Lower Bartonian of Switzerland, and Biarritz, Upper Bartonian of Biarritz, Upper Mokattam of Egypt, Upper Eocene of the Balkans, Eocene of Biarritz (type locality for *tarbelliana*), La Palarea (type locality for *laevis*), Istria, Hungary, and the northern Alps, Upper Priabonian of Italy, and Biarritz, Oligocene or Eocene of Austria, Tongrian of France, and Italy, Oligocene of the Phare de Biarritz, Schio Beds (Aquitanian) of Dego

REMARKS *Teredo intestinoides* Cossmann & Pissarro, from the Ranikot of Western Pakistan, is evidently to be regarded as a synonym of *T tournali* Leymerie The intestine-like manner of coiling is by no means characteristic, such forms often being accompanied by others of the same diameter and general appearance and which are almost straight and unwrinkled *Septaria tarbelliana* d'Archiac also appears to be indistinguishable from Leymerie's species, *S tarbelliana* was founded on fig 2 of Leymerie's *Teredo tournali* Frauscher (1886) included *T argonnensis* d'Orbigny as figured by Schafhautl (1863, p 178, Pl 44, figs 8*a*,*b*) in the synonymy of *T tournali*, but Schafhautl's illustrations show a form that is much too large for *T tournali*, and his form is evidently quite distinct *T subparisiensis* de Gregorio (see de Gregorio, 1894*b*, p 37, Pl 6, figs 187, 188, Fabiani, 1915, pp 259, ?262), recorded tentatively by Dainelli (1915, p 493, Pl 47, figs 29–35) under the same name, and recorded as *T tournali* Leymerie var *subparisiensis* de Gregorio by de Gregorio (1896, p 85, Pl 13, figs 1–3), has been recorded from the Lutetian and Auversian of Venetia (Monte Postale is the type locality), and is evidently closely related Some authors have placed it in the synonymy of *T tournali* The fine, serrate, concentric annulations are the only feature distinguishing it from *T tournali*, and it seems possible that these may be developed by weathering Only by an examination of the actual specimens and of the fossils associated with them at the localities from which *subparisiensis* has been recorded can it be decided whether this form is a synonym of *T tournali* or not

Schlosser (1925*a*) included *Schafhautlia kressenbergensis* Naegeli, in Schafhäutl, 1863, p 29, Pl 65, figs 1–4, in the synonymy of *Teredo tournali*, this was obviously a *lapsus calami*, as *Schafhautlia* is a plant—the name, incidentally, does not seem to be in the index of plant generic names

Superfamily PANDORACEA

Family LYONSIIDAE

Genus *LYONSIA* Turton, 1822

(*Conch Insul Brit* **17**, 34)

TYPE SPECIES *Mya striata* Montagu, Recent = *Lyonsia norvegica* (Gmelin & Chemnitz), monotypy

SYNONYMS *Magdala* Leach, *teste* Brown, 1827 (*Ill Conch G B and I* Pl 11, fig 1), type species *Magdala striata* (Montagu), Recent, monotypy

Hiatella Brown, 1827 (*Ill Conch G B and I* Pl 16, fig 26) *non* Daudin, in Bosc, 1801 (Moll), type species *H striata* (Montagu), Recent, monotypy

'*Tetragonoste*' Deshayes, 1830 (*Enc Méth* **2**, 590) (not binomial)

Myatella Brown, 1833 (*Conch Text Book*, p 142), type species *M striata* (Montagu), Recent, monotypy

Pandorina Scacchi, 1833 (*Osserv Zool* p 15) *non* Bory de St Vincent, 1827 (Prot), type species to be selected from *Tellina coruscans* S d Chiaje, Recent and *T papyracea* P, Recent

Tetragonostea (Deshayes) Herrmannsen, 1849 (*Index Gen Malac* **2**, 565) (= *Lyonsia*)

Eudorina Pascher, 1926 (*Arch Protistenk* **53**, 470, 471) *non* Ehrenberg, 1832 (Prot) *nec* Snellen, 1895 (Lep) (= *Pandorina* Scacchi)

LYONSIA PAKISTANICA n sp

(Figures 91 *a*, *b*, plate 14)

MATERIAL *Rakhi Nala section* Lower Chocolate Clays (local zone 10) (FB F 1967, the holotype, Reg No L 80405, and *10*+ topotypes, Reg No L 80406–11)

DESCRIPTION Shell transversely subelliptical, nuculaniform, thin-shelled, showing no trace of having possessed taxodont teeth, gently to moderately inflated, apparently somewhat nacreous internally Umbos small, pointed, erect, not prominent, situated a little anterior to the middle line, from one-third to five-twelfths of the length Antero-dorsal margin relatively short, very slightly convex, moderately descendent Anterior end moderately narrowly rounded Ventral margin gently to moderately convex Posterior end subrostrate, a little produced, its lower margin gently convex and merging insensibly into the ventral margin, meeting the postero-dorsal margin in a rounded angle of about 90° Postero-dorsal margin relatively long, practically straight, gently descendent Valve margins internally smooth Surface almost smooth, but ornamented with vague concentric threads which are more noticeable in the umbonal region (where there are 4 in ¾ mm, and where they appear to attain at most one-third of the width of their intervals), and with vague, rather closely spaced, somewhat irregular radial threads

DIMENSIONS Holotype length 10 9 mm, height 5 25 mm

REMARKS This species seems to be very similar indeed to fig 14 of Roedel's *Lyonsia baltica* from the Palaeogene of north Germany (Turritella beds of Hiddensee) Roedel's fig 15 (1935, p 34, Pl 1) is the type of the species, and is an elongate, posteriorly truncate and bicarinate form seemingly specifically distinct from the specimen illustrated in fig 14, which is not truncated or carinate posteriorly Roedel's fig 14, while obviously very close to the Pakistan form, does seem to be more narrowly transverse.

Family PHOLADOMYIDAE

Genus *PHOLADOMYA* G B Sowerby, 1823

(*Gen Shells* (19))

TYPE SPECIES *Pholadomya candida* Sowerby, Recent, Gray, 1847

SYNONYM *Procardia* Meek, 1871 (*Proc Acad Nat Sci Philad* p 184), type species *Isocardia? hodgei* Meek, Cretaceous, original designation

PHOLADOMYA sp A

(Figures 127*a*,*b*, plate 17)

MATERIAL *Rakhi Nala section* Shales with Alabaster (local zone 7) (FB F 1925, the holotype, Reg No L 80412, a mould on which the ornament is not preserved)

DESCRIPTION Shell of moderately large size, moderately strongly inflated, subrectangular in outline Umbos small, moderately prominent, situated well anterior to the middle line at about one-quarter of the length Antero-dorsal margin short, gently convex, rather steeply descendent Anterior end rounded, apparently slightly truncated on the specimen under examination, the appearance possibly due to weathering Ventral margin subhorizontal, moderately long, slightly convex Posterior end broken, evidently not strongly produced, rather short Postero-dorsal margin moderately long, straight, horizontal

DIMENSIONS Holotype length 31 1 mm (incomplete), height 28 1 mm , thickness (both valves) 18 4 mm

REMARKS This species is much less elongate, less cuneiform, higher, and blunter posteriorly than the Ranikot species *Pholadomya halaensis* d'Archiac & Haime (1854, p 233, Pl 16, figs 1,*a*) Incidentally, Douvillé's illustrations of *P halaensis* d'Archiac & Haime (1929, p 67, Pl 11, figs 6, 7), from the *Cardita beaumonti* beds of Western Pakistan, are specifically distinct from d'Archiac & Haime's species, the shell being less cuneiform, relatively higher, and with a more subrectangular appearance Douvillé's form is, however, not so short as *Pholadomya* sp A, which may be the same as an unidentified species of *Pholadomya* (Reg No L 56026) in the collections in the Natural History Museum, believed possibly to come from the Laki series of Sind The latter form, while not nearly so narrow posteriorly as the type of *P halaensis*, has wider spaced, and much more oblique radial ribs compared with the *Cardita beaumonti* beds form illustrated by Douvillé *Pholadomya nummulitica* Frauscher (1886, p 228, Pl 11, fig 2), from the Eocene of the northern Alps, is more elongate and more pointed posteriorly, and the radial ribs are not so oblique as in the specimen L 56026 *P ludensis* Deshayes, as figured by Cossmann & Pissarro (1904*a*, Pl 4, fig 28–4), from the Bartonian of Ludes, is less cuneiform, not so high posteriorly, and less quadrate *P virgulosa?* Sowerby as figured by Deshayes (1856, Pl 9, figs 9, 10), from the Lower Sands of Laon, is less rectangular in outline

Superfamily Poromyacea

Family Poromyidae

Genus *NEAEROPOROMYA* Cossmann, 1886

(*Ann Soc Malac Belg* **21**, 58)

Type species *Corbula argentea* Lamarck, Eocene, original designation and monotypy

NEAEROPOROMYA PAKISTANICA n sp

(Figures 92*a*, *b*, *c*, plate 14)

Material *Zinda Pir section* Upper Chocolate Clays (lower part, local zone 12) (FB F 2541, the holotype, Reg No L 80413)

Description Shell fairly small, corbuliform, posteriorly rostrate, body of shell strongly inflated, inequivalve, right valve the larger Umbos rather acute and prominent, inflated, prosogyrous, submedian, situated very slightly anterior to the middle line Antero-dorsal margin of moderate length, very slightly convex, moderately steeply descendent Anterior end rounded Ventral margin fairly strongly convex, a little straighter posteriorly Posterior end bluntly rostrate, a little produced, end of rostrum gently convex, not long, sloping upwards gently towards the umbos, meeting the adjacent margins in blunt obtuse angles of which the upper is the larger Postero-dorsal margin of moderate length only, straight, gently descendent Surface with two fine, sharp, distinct, raised threads or fine carinae extending from the umbo to the postero-ventral region, one to the postero-ventral corner, the other to a position further back and limiting the inflated portion of the shell Anterior carina nearly vertical, sloping downwards a little towards the posterior end, posterior carina distinctly more oblique Surface ornamented with distinct, strong, concentric threads, 3 to 4 in ¾ mm, the intervals being of the same width as or slightly wider than the threads No apparent gape

Dimensions Holotype length 6 0 mm, height 4 75 mm, thickness (both valves) 4 0 mm

Remarks *Neaeroporomya argentea* (Lamarck) as figured by Glibert, 1936 (p 200, fig 71), from the Wemmel Sands of Zellick (Belgium)—and also from the Lutetian of France, the Auversian of France, the lower Upper Bracklesham Beds of England, and the Lattorfian of Germany—is less globose, with a more differentiated rostrum, is less sharply rounded anteriorly, and has less uniform concentric ornament *Corbula argentea* Lamarck as figured by Nyst (1843, Pl 3, fig 5) has a more produced and more differentiated rostrum, is less inflated, and has more closely spaced concentric ornament *Cuspidaria tricostata* Slodkewitsch (1928, p 559, Pl 39, figs 2, 3), from the Palaeogene of the Donetz basin, has a distinctly more pointed rostrum, more closely spaced concentric ornament, and often has a third radial carina. *C lutulenta* Rovereto (1914, p 159, Pl 5, fig 8), from the Oligocene of Liguria, while similar in size and form, shows no concentric ornament, has no radial carinae limiting the rostral area, and has a more constricted rostrum The general appearance, and especially the two posterior radial carinae, place the Pakistan species as a *Neaeroporomya* rather than a *Cuspidaria*

NEAEROPOROMYA SORIENSIS n sp

(Figures 93*a*, *b*, *c*, plate 14)

Material *Zinda Pir section* Upper Chocolate Clays (upper part, local zone 14) (FB F 2511, the holotype, Reg No L 80414)

Description Shell rather small, subequivalve, nuculaniform, inflation only moderate Umbos small, distinct, prominent, slightly prosogyrous, submedian, situated slightly anterior to the middle line at about two-fifths of the length Posterior end with a short, bluntly pointed rostrum Antero-dorsal margin of moderate length, straight or slightly concave, rather steeply descendent Anterior end rounded, somewhat angular at its junction with the antero-dorsal margin Ventral margin strongly convex, not becoming so vertical posteriorly as anteriorly, posterior end not very produced, obliquely truncate, short, sloping upwards very obliquely towards the umbos, forming an angle of about 90° with the ventral margin, and a very obtuse angle with the postero-dorsal margin Postero-dorsal margin moderately long, straight, slightly descendent Two distinct, radial carinae run from the umbo to the postero-ventral border of the shell, the posterior one goes to the postero-ventral corner, and the anterior one, which is slightly convex forwards, goes to a point about two-thirds of the length of the ventral margin from its anterior end The strong, concentric threads, about 5 in ¾ mm , have intervals of the same width as or slightly wider than the threads

Dimensions Holotype length 2 8 mm , height 2 0 mm , thickness (both valves) 1 5 mm

Remarks *Neaeroporomya argentea* (Lamarck), as figured by Glibert (1936, p 200, fig 71), from the Wemmel Sands of Zellick (Belgium), etc , has higher umbos, a less convex ventral margin, and the two radial carinae are less widely spaced Cossmann & Pissarro's illustration of the species (1904*a*, Pl 4, fig 26–1), from the Lutetian of Parnes and from the Bartonian, shows a form which is less produced and less rostrate posteriorly, and in which the posterior margin is longer and more steeply sloping *N pakistanica* is distinctly more convex, more inequivalve, larger, more corbuliform, and more regularly rounded anteriorly, and the anterior radial carina is more posteriorly placed and is straight

Genus *PSEUDOCUSPIDARIA* n g

Type species *Cuspidaria lakiensis* Cox, Lower Eocene

Generic characters Size moderate, distinctly larger than members of the Cuspidariidae, subequivalve, posteriorly rostrate, ornamented with strong concentric folds, very thin-shelled, probably internally nacreous (judging from a well-preserved specimen from Sind)

PSEUDOCUSPIDARIA LAKIENSIS (Cox), 1938

References *Cuspidaria lakiensis* Cox, 1938*b* (p 170, Pl 7, fig 3)

Material *Rakhi Nala section* Upper Rakhi Gaj Shales (local zone 4) (FB F. 1853, *1*, FB F 1855, *1*), Green and Nodular Shales (local zone 6) (FB F 1899, *2*, FB F 1900, *10+*, FB F 1902, *2*, FB F 1903, *2*), Rubbly Limestones (local zone 6) (FB. F. 1909, *1*, FB F 1910, *1*, FB F 1912, *10+*, Reg No. L 80415–20, FB. F 1914, *2*, FB. F 1915, *2*, FB F 1918, *1*), Shales with Alabaster (local zone 6) (FB F 1919, *1*), Shales with Alabaster (local zone 7) (FB F 1931, *2*, FB F 1938, *2*, FB F 1943, *1*), *Kohat area* (*Tarkhobi section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2171, *2*, FB F 2173, *15*+), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2175, *5*), *Kohat area* (*Panoba section*) Middle Shekhan Limestone (local subzone 3*b*) (FB F 2230, *2*, FB F 2294, *15*+), Upper Shekhan Limestone (local subzone 3*b*) (FB F 2289, *15*+, FB F 2290, *4*, FB F 2291, *15*+)

FURTHER DISTRIBUTION IN PAKISTAN Ghazij Shales south of Nila Kund (Dera Ghazi Khan, type locality), Laki (174 ft below gypsum) of the Panoba Nala

REMARKS Cox has already indicated that this species belongs to a unique group The very thin shell, relatively large size, and general appearance distinguish it from all other members of the Cuspidariidae known to the writer, and it seems best placed under a new generic name in the closely allied family Poromyidae

Family CUSPIDARIIDAE

Genus *CUSPIDARIA* Nardo, 1840

(*Rev zool* p 30)

TYPE SPECIES *Cuspidaria typus* Nardo, Recent = *Tellina cuspidata* Olivi = *Mya rostrata* Spengler, Dall, 1886

SYNONYMS *Neaera* Griffith & Pidgeon, in Cuvier, 1834 (*Anim Kingd*, *Moll*, *etc*, **12**, Pl 22) *non* Robineau-Desvoidy, 1830 (Dipt), type species *N chinensis* Griffith & Pidgeon, in Cuvier, Recent, monotypy

Neroea Griffith & Pidgeon, in Cuvier, 1834 (*Anim Kingd*, *Moll*, *etc*, p 598) (error)

Neara Gray, 1839 (*Rep Brit Assoc* (*Newcastle* 1838), 8, Trans p 110) (error)

Subgenus *CARDIOMYA* A Adams, 1864

(*Ann Mag Nat Hist* (3), **13**, 208)

TYPE SPECIES *Neaera gouldiana* Hinds, Recent, monotypy

SYNONYM *Spathophora* Jeffreys, 1882 (*Proc Zool Soc Lond* 1881, p 943) *non* Amyot & Serville, 1843 (Hem), type species if not yet selected, to be chosen from *Neaera curta* Jeffreys, Recent, *Corbula costellata* Deshayes, Miocene-Recent, and *Neaera striata* Jeffreys, Recent

CUSPIDARIA (*CARDIOMYA*) *SORIENSIS* n sp

(Figures 94*a*, *b*, *c*, plate 14)

MATERIAL *Zinda Pir section* Lower Chocolate Clays (local zone 10) (FB F 2564, *1*), Upper Chocolate Clays (lower part, local zone 12) (FB F 2539, *1*, FB F 2536, the holotype, Reg. No L 80421, and 4 topotypes, Reg No L 80422–5)

DESCRIPTION Shell small, moderately robust for its size, corbuliform, posteriorly with a small, distinct rostrum, body of shell strongly inflated, slightly inequivalve, the left valve being the larger Umbos prominent, submedian, gently opisthogyrous Antero-dorsal margin of moderate length, slightly to gently convex, rather steeply descendent Anterior end rounded, vaguely angular at its junction with the antero-dorsal margin Ventral margin strongly convex Rostrum short, situated high up, forming a rounded, acute angle, its upper margin horizontal Ornament consisting of strong radial ribs of varying strength and of fine concentric threads Ribs confined to the body of the shell, not extending on to the rostrum, there being 6 in a distance of ¾ mm along the ventral margin About 25 ribs on the body of the shell, and 2 close to the dorsal margin of the rostrum, of the 25, 6 are distinctly more prominent and well-marked than the remainder, the distinction being most noticeable on the posterior half of the shell Ribs distinctly beaded, and also crossed by fine concentric threads of which there are 8 in ¾ mm ventrally, these threads are continuous over the whole of the rostrum

Dimensions Holotype length 2 6 mm , height 2 1 mm , thickness (both valves) 1 69 mm

Remarks Compared with *Neaera reticosa* von Koenen (1868*a*, p 265, Pl 30, fig 3), from the Middle Oligocene of Hermsdorf, *Cuspidaria* (*Cardiomya*) *soriensis* is more transverse, has the ribs extending over the anterior part of the shell, some of the ribs are stronger than others, and the ribs are all beaded

CUSPIDARIA (*CARDIOMYA*) sp A

(Figures 95*a*, *b*, plate 14)

Material *Rakhi Nala section* Upper Chocolate Clays (upper part, local zone 13) (FB F 1986, the holotype, Reg No L 80426, and 1 topotype, Reg No L 80427, FB F 1987, *1*)

Description Shell small, obliquely suboval, the longer axis being that from the umbo to the antero-ventral region, with a small rostrum situated high up posteriorly, body of shell strongly inflated Umbos small, not prominent, gently opisthogyrous, situated posterior to the middle line at about one-third of the length Antero-dorsal margin rather short, slightly convex, moderately descendent Anterior end convex, rather oblique, joining the ventral margin in a moderately sharply rounded curve Ventral margin rather convex, steeply ascendent posteriorly, there is a concave region where it joins the rostrum Rostrum short, triangular, situated very high up, its upper margin horizontal Shell ornamented with some 25 subequal radial ribs, which do not extend on to the rostrum

Dimensions Holotype length 2 25 mm , height 1 88 mm , thickness (both valves) 1 3 mm

Remarks These specimens, which are all moulds, differ from *Cuspidaria* (*Cardiomya*) *soriensis* n sp , in having ribs of uniform size, and in their obliquely oval outline

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DESCRIPTION OF PLATES

PLATE 9

FIGURE 1 *Nucula domandaensis* n sp *a*, left valve (× 2), *b*, dorsal view (× 2) Eocene 4 miles north of Domanda Reg No L 77877, holotype

FIGURE 2 *Nucula* (*Lamellinucula*) *pakistanica*, n sp *a*, left valve ($\times 6\frac{7}{8}$), *b*, dorsal view ($\times 6\frac{7}{8}$) Lower Chocolate Clays Zinda Pir Reg No L 79793, holotype

FIGURE 3 *Nucula* (*Lamellinucula*) *costacallistiformis*, n sp *a*, right valve ($\times 6\frac{1}{2}$), *b*, dorsal view ($\times 6\frac{1}{2}$) Ghazij Shales Zinda Pir Reg No L 79799, holotype

FIGURE 4 *Nucula* (*Lamellinucula*) *depressilunulata*, n sp *a*, right valve (× 1), *b*, right valve (× 1) Upper Chocolate Clays Zinda Pir Reg No L 79806, holotype

FIGURE 5 *Nucula* (*Lamellinucula*) *soriensis*, n sp *a*, *b*, *c*, right valve ($\times 6\frac{7}{8}$) Ghazij Shales Zinda Pir Reg No L 79811, holotype

FIGURE 6 *Nucula* (*Gibbonucula*) *corbuliformis*, n subg et n sp *a*, right valve, the holotype, Reg No L 79816 ($\times 7\frac{1}{2}$), *b*, left valve, a topotype, Reg No L 79817 ($\times 6\frac{5}{8}$), *c*, dorsal view of holotype ($\times 7\frac{1}{10}$) Ghazij Shales Zinda Pir

FIGURE 7 *Leionucula punjabensis*, n sp *a*, left valve ($\times \frac{15}{16}$), *b*, part of ornament enlarged, *c*, dorsal view ($\times \frac{15}{16}$) Upper Chocolate Clays Zinda Pir Reg No L 79832, holotype

FIGURE 8 *Leionucula pakistanica*, n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Lower Chocolate Clays Zinda Pir Reg. No L 79833, holotype.

Figure 9 *Nuculana* (*Saccella*)(?) *rakhiensis*, n sp Left valve (× 1½) Green and Nodular Shales Rakhi Nala Reg No L 79842, holotype

Figure 10 *Nuculana* (*Saccella*) *hamata*, n sp *a*, left valve (× 7), Reg No L 79843, holotype, *b*, dorsal view of holotype (× 7), *c*, left valve (× 7), Reg No L 79844, topotype Upper Chocolate Clays Rakhi Nala

Figure 11 *Nuculana* (*Saccella*) *pakistanica*, n sp *a*, left valve (× $6\frac{7}{10}$), *b*, dorsal view (× $6\frac{7}{10}$) Lower Chocolate Clays Rakhi Nala Reg No L 79850, holotype

Figure 12 *Nuculana* (*Saccella*) *semibistriata*, n sp Left valve (× 6⅞) Green and Nodular Shales Rakhi Nala Reg No L 79851, holotype

Figure 13 *Nuculana* (*Saccella*) *punjabensis*, n sp *a*, right valve (× 6½), *b*, dorsal view (× 6½) Upper Chocolate Clays Zinda Pir Reg No L 79854, holotype

Figure 14 *Nuculana* (*Saccella*) *umboni-inflata* n sp *a*, right valve (× 7), *b*, dorsal view (× 7) Upper Chocolate Clays Zinda Pir Reg No L 79855, holotype

Figure 15 *Nuculana* (*Saccella*) *soriensis*, n sp *a*, left valve (× $6\frac{13}{16}$), *b*, dorsal view of left valve (× $6\frac{13}{16}$) Ghazij Shales Zinda Pir Reg No L 79857, holotype

Figure 16 *Nuculana* (*Saccella*) *soriensis*, n sp *a*, right valve (× 10¼), *b*, dorsal view (× 5¾) Ghazij Shales Zinda Pir Reg No L 79864, syntype

Figure 17 *Barbatia* (*Plagiarca*) *pseudonavicula*, n sp *a*, right valve (× 6), *b*, dorsal view (× 4½) Lower Chocolate Clays Rakhi Nala Reg No L 79867, holotype

Figure 18 *Glycymeris*(?) *soriensis*, n sp *a*, left valve (× 6¾), *b*, dorsal view (× 6¾) Upper Chocolate Clays Zinda Pir Reg No L 79874, holotype

Figure 19 *Noetia magnifica*, n sp *a*, right valve (1), *b*, dorsal view (× 1) Lower Chocolate Clays east of Safaed, south of Tobah, Dera Ghazi Khan District Reg No L 77886, holotype

Figure 20 *Noetia magnifica*, n sp Left valve (× ¾) Lower Chocolate Clays Rakhi Nala Reg No L 79876, syntype

Figure 21 *Arcopsis sparsiincisa*, n sp *a*, left valve (× 10¼), *b*, dorsal view of left valve (× 10) Upper Chocolate Clays Zinda Pir Reg No L 79881, holotype

Figure 22 *Arcopsis*(?) sp A *a*, right valve (× 10½), *b*, right valve (internal view) (× 10½) Ghazij Shales Zinda Pir Reg No L 79882, holotype

Figure 23 *Chlamys soriensis* n sp Left valve (× 1⅝) Upper Chocolate Clays Zinda Pir Reg No L 79927, holotype

Figure 24 *Musculus* (*Undatimusculus*) *rakhiensis*, n subg et n sp Right valve (× 1½) Green and Nodular Shales Rakhi Nala Reg No L 79985, holotype

Figure 25 *Venericardia* sp B *a*, right valve (× 1), *b*, section of ribs (enlarged), *c*, dorsal view (× 1) Green and Nodular Shales Rakhi Nala Reg No L 80023, holotype

Figure 26 *Crenella antero-divaricata*, n sp *a*, left valve (× 10⅝), *b*, anterior view of left valve (× 10⅝) Ghazij Shales Zinda Pir Reg No L 79991, holotype

Figure 27 *Venericardia pakistanica*, n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Upper Rakhi Gaj Shales Rakhi Nala Reg No L 80012, holotype

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Figure 28. *Nucula* (*Lamellinucula*) *depressilunulata*, n sp End view (× 1) Upper Chocolate Clays Zinda Pir. Reg No L 79807, topotype

Figure 29. *Leionucula rakhiensis*, n sp *a*, left valve (× 1), *b*, part of ornament, enlarged, *c*, dorsal view (× 1) Reg No. L 79825, holotype *Venericardia* Shales Rakhi Nala.

Figure 30 *Solemya insignifica*, n sp Right valve (× 1) Upper Rakhi Gaj Shales Rakhi Nala. Reg No L 79866, holotype

Figure 31 *Glycymeris* sp A *a*, right valve (× 21), *b*, section of ribs (enlarged), *c*, dorsal view (× 21). Ghazij Shales Zinda Pir Reg No L 79875, holotype

Figure 32 *Cucullaea*(?) sp A *a*, right valve (× 19), *b*, dorsal view (× 19) Ghazij Shales Zinda Pir Reg No L 79884, holotype

Figure 33 *Vulsella pakistanica*, n sp *a*, left valve (× 1), *b*, ornament enlarged Shales with Alabaster Rakhi Nala Reg No L 79885, holotype

Figure 34 *Vulsella grandicubitus*, n sp *a*, left valve (× ½), *b*, dorsal view (× ½) White Marl Band Zinda Pir Reg No L 79887, holotype

Figure 35 *Vulsella* sp A Left valve (× 1) Upper Chocolate Clays Rakhi Nala Reg No L 79894, holotype

Figure 36 *Vulsella* sp B Right valve (× 1) *Pellatispira* Beds Rakhi Nala Reg No L 79896, topotype

Figure 37 *Vulsella* sp B Left valve (× 1) *Pellatispira* Beds Rakhi Nala Reg No L. 79895, holotype

Figure 38 *Vulsella* sp B Two end views (× 1) *Pellatispira* Beds Rakhi Nala Reg No L 79897, topotype

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Figure 39 *Pinna punjabensis* n sp *a*, right valve (× 1), *b*, cross section (× 1) Ghazij Shales south of Nila Kund, Dera Ghazi Khan District Reg No L 77898, holotype

Figure 40 *Pinna shekhanensis*, n sp Right valve (× ½) Lower Shekhan Limestone Shekhan Nala Reg No L 79908, holotype

Figure 41 *Anomia interrupta* n sp *a*, ?left valve (× 1), *b*, ornament enlarged, *c*, dorsal view Shales with Alabaster Rakhi Nala Reg No L 79909, holotype

Figure 42 *Anomia pakistanica* n sp *a*, single valve (× 1), *b*, ornament enlarged Lower Chocolate Clays Zinda Pir Reg No L 79911, holotype

Figure 43 *Chlamys pakistanica* n sp Right valve (× 1) *Pellatispira* Beds Zinda Pir Reg No L 79928, holotype

Figure 44 *Amusium* (*Entoliopsis*) *uniradiatum* n subg et n sp *a*, right valve, external view (× 2), *b*, right valve, internal view (× 2), *c*, right valve, dorsal view (× 2) Green and Nodular Shales Rakhi Nala Reg No L 79932, holotype

Figure 45 *Amusium* (*Entoliopsis*) *uniradiatum* n subg et n sp *a*, left valve, external view (× 2), *b*, left valve, internal view (× 2), *c*, section of ridges bordering ear (enlarged), *d*, ridges bordering ear (enlarged) Green and Nodular Shales Rakhi Nala Reg No L 79933, topotype

Figure 46 *Spondylus subaequivalvis*, n sp *a*, side view (× 1), *b*, lateral view of a spine (enlarged), *c*, dorsal view (× 1) White Marl Band Zinda Pir Reg No L 79942, holotype

Figure 47 *Dimya rakhiensis* n sp Right valve (× 2). Upper Chocolate Clays Rakhi Nala Reg No L 79943, holotype

Figure 48 *Dimya rakhiensis* n sp Interior view (× 2) Upper Chocolate Clays Rakhi Nala Reg No L 79944, topotype

Figure 49 *Dimya rakhiensis* n sp *a*, interior view (× 2½), *b*, internal ribs enlarged. Upper Chocolate Clays Rakhi Nala Reg No L 79945, topotype

Figure 50 *Ostrea rakhiensis* n sp Left valve (× 1) Green and Nodular Shales Rakhi Nala. Reg. No L 79966, holotype

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Figure 51 *Dimya*(?) *spondyliformis* n sp Right valve (× 3) Upper Chocolate Clays Rakhi Nala Reg No. L 79949, holotype

Figure 52 *Dimya*(?) *spondyliformis* n sp *a*, right valve (× 3), *b*, left valve (× 3), *c*, ornament enlarged, *d*, end view (× 3) Upper Chocolate Clays Rakhi Nala Reg No L 79950, topotype

Figure 53 *Dimya*(?) *spondyliformis* n sp Left valve, internal view (× 3) Upper Chocolate Clays Rakhi Nala Reg No L 79951, topotype

Figure 54 *Ostrea pseudopunica* n sp *a*, left valve, external view (× 1), *b*, left valve, internal view (× 1) Lower Chocolate Clays east of Safaed, south of Tobah, Dera Ghazi Khan District Reg No L 77893, holotype

Figure 55 *Ostrea pseudopunica* n sp Left valve (× 1) Lower Chocolate Clays east of Safaed, south of Tobah, Dera Ghazi Khan District Reg No L 77889, topotype

Figure 56 *Ostrea pseudopunica* n sp Left valve (× 1) Lower Chocolate Clays east of Safaed, south of Tobah, Dera Ghazi Khan District Reg No L 77891, topotype

Figure 57 *Ostrea pseudopunica* n sp Right valve (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 79961, syntype

Figure 58 *Ostrea* (*Liostrea*) *pseudoflemingi* n sp Left valve (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 79967, holotype

Figure 59 *Ostrea* (*Liostrea*) *pseudoflemingi* n sp Left valve (× 1) Lower Chocolate Clays Zinda Pir Reg No L 79968, syntype

Figure 60 *Ostrea* (*Liostrea*) *pseudoflemingi* n sp *a*, right valve, external view (× 1), *b*, right valve, internal view (× 1) Lower Chocolate Clays Zinda Pir Reg No L 79969, syntype

Figure 61 *Ostrea* (*Liostrea*) *pseudoflemingi* n sp Left valve (× 1) Lower Chocolate Clays Zinda Pir Reg No L 79973, syntype

Figure 62 *Ostrea* (*Liostrea*) *pseudoflemingi* n sp *a*, left valve (× 1), *b*, right valve (× 1), *c*, part of ornament enlarged, *d*, dorsal view (× 1) Lower Chocolate Clays Zinda Pir Reg No L 79912, syntype

Figure 63 *Ostrea* (*Lopha*) *melania* d'Orbigny *a*, left valve (× 1), *b*, right valve (× 1), *c*, dorsal view (× 1) Upper Chocolate Clays Rakhi Nala Reg No L 79974, homoeotype

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Figure 64 *Musculus punjabensis* n sp *a*, left valve (× 2), *b*, dorsal view of left valve (× 2) Shales with Alabaster Rakhi Nala Reg No L 79984, holotype

Figure 65 *Venericardia soriensis* n sp *a*, left valve (× 1), *b*, cross-section of ribs (enlarged), *c*, longitudinal section of rib (enlarged), *d*, dorsal view (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80019, holotype

Figure 66 *Venericardia trachycardiiformis* n sp *a* right valve (× 1), *b*, cross-section of ribs (enlarged), *c*, longitudinal section of ribs (enlarged), *d*, dorsal view (× 1) Upper Chocolate Clays Zinda Pir Reg No. L 80020, holotype

Figure 67 *Venericardia* (*Pteromeris*) (?) *umboniperdita* n sp *a*, right valve (× 19¼), *b*, dorsal view (× 20¾) Lower Chocolate Clays Zinda Pir Reg No L 80021, holotype

Figure 68 *Venericardia* sp A *a*, left valve (× 1), *b*, dorsal view (× 1) Green and Nodular Shales Rakhi Nala Reg No L 80022, holotype

Figure 69 *Diplodonta pakistanica* n sp *a*, left valve (× 1), *b*, right valve (× 1), *c*, dorsal view (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 80036, holotype.

Figure 70 *Diplodonta sonensis* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Lower Chocolate Clays Zinda Pir Reg No L 80043, holotype

Figure 71 *Diplodonta*(?) *punjabensis* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) White Marl Band Zinda Pir Reg No L 80047, holotype

Figure 72 *Diplodonta* sp A Left valve (× 1) Lower Chocolate Clays Zinda Pir Reg No L 80053, holotype

Figure 73 *Diplodonta* sp. A Left valve (× 1) Lower Chocolate Clays Zinda Pir Reg No L 80054, topotype

Figure 74 *Lucina exquisita* n sp *a*, left valve (× 2), *b*, dorsal view (× 2) Ghazij Shales Zinda Pir Reg No L 80064, holotype

Figure 75 *Phacoides pakistanicus* n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 80067, holotype

Figure 76 *Tellina pakistanica* n sp *a*, left valve (× 1), *b*, ornament enlarged *Venericardia* Shales Rakhi Nala Reg No L 80207, holotype

Figure 77 *Tellina rakhiensis* n sp *a*, left valve (× 1), *b*, ornament enlarged Upper Rakhi Gaj Shales Rakhi Nala Reg No L 80208, holotype

Figure 78 *Tellina* (*Eurytellina*) *gypsifera* n sp *a*, dorsal view (× 1), *b*, left valve (× 1) Shales with Alabaster Rakhi Nala Reg No L 80213, holotype

Figure 79 *Macoma sonensis* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Lower Chocolate Clays Zinda Pir Reg No L 80223, holotype

Figure 80 *Macoma ovatitriangularis* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Lower Chocolate Clays Zinda Pir Reg No L 80231, holotype

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Figure 81 *Lucina rakhiensis* n sp *a*, left valve (× $1\frac{3}{8}$), *b*, dorsal view (× 1) Rubbly Limestones Rakhi Nala Reg No L 80056, holotype

Figure 82 *Lucina* (*Bellucina*) *praeagassizi*, n sp *a*, left valve (× $6\frac{1}{4}$), *b*, dorsal view (× $6\frac{3}{4}$) Upper Chocolate Clays Zinda Pir Reg No L 80066, holotype

Figure 83 *Discors sonensis* n sp Left valve (× 1) *Pellatispira* Beds Zinda Pir Reg No L 80278, holotype

Figure 84 *Macrocallista* (*Costacallista*) *punjabensis* n sp *a*, right valve (× $\frac{3}{4}$), *b*, dorsal view (× $\frac{3}{4}$) Upper Chocolate Clays Zinda Pir Reg No L 80334, holotype

Figure 85 *Azorinus* (*Zoziella*) *punjabensis* n subg et n sp Right valve (× $1\frac{1}{2}$) Upper Rakhi Gaj Shales Rakhi Nala Reg No L. 80358, holotype

Figure 86 *Corbula rakhiensis* n sp *a*, left valve (× $6\frac{3}{8}$), *b*, dorsal view (× $6\frac{3}{8}$) Upper Chocolate Clays Rakhi Nala Reg No L 80362, holotype

Figure 87 *Corbula sonensis* n sp *a*, right valve (× $3\frac{1}{10}$), *b*, left valve (× $3\frac{1}{10}$), *c*, dorsal view (× $3\frac{1}{10}$) Lower Chocolate Clays Zinda Pir Reg No L 80369, holotype

Figure 88 *Corbula punjabensis* n sp *a*, right valve (× $1\frac{1}{2}$), *b*, left valve (× $1\frac{1}{2}$), *c*, dorsal view (× $1\frac{1}{2}$) Ghazij Shales Zinda Pir Reg No L 80371, holotype

Figure 89 *Corbula pseudorakhiensis* n sp *a*, right valve (× 7), *b*, left valve (× 7), *c*, dorsal view (× 7) Ghazij Shales Zinda Pir Reg No L 80372, holotype

Figure 90 *Corbula* (*Varicorbula*) *pseudopisum* n sp Right valve (× $6\frac{3}{8}$) *Pellatispira* Beds Rakhi Nala Reg No L 80384, holotype

Figure 91 *Lyonsia pakistanica* n sp *a*, left valve (× 1⅜), *b*, dorsal view of left valve (× 1⅜) Lower Chocolate Clays Rakhi Nala Reg No L 80405, holotype

Figure 92 *Neaeroporomya pakistanica* n sp *a*, right valve (× 4), *b*, left valve (× 4), *c*, dorsal view (× 4) Upper Chocolate Clays Zinda Pir Reg No L 80413, holotype

Figure 93 *Neaeroporomya soriensis* n sp *a*, right valve (× 7½), *b*, left valve (× 7½), *c*, dorsal view (× 7½) Upper Chocolate Clays Zinda Pir Reg. No L 80414, holotype

Figure 94 *Cuspidaria* (*Cardiomya*) *soriensis* n sp *a*, right valve (× 6 17/20), *b*, left valve (× 6 17/20), *c*, dorsal view (× 6 17/20) Upper Chocolate Clays Zinda Pir Reg No L 80421, holotype

Figure 95 *Cuspidaria* (*Cardiomya*) sp A *a*, left valve (× 6½), *b*, dorsal view (× 6½) Upper Chocolate Clays Rakhi Nala Reg No L 80426, holotype

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Figure 96 *Macoma safaedensis* n sp *a*, left valve (× 1), *b*, ornament enlarged, *c*, dorsal view (× 1) Lower Chocolate Clays east of Safaed, south of Tobah, Dera Ghazi Khan District Reg No L 77888, holotype

Figure 97 *Macoma safaedensis* n sp *a*, right valve (× 1), *b*, ornament enlarged, *c*, dorsal view (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 80215, syntype

Figure 98 *Macoma panobaensis* n sp *a*, dorsal view (× 1), *b*, right valve (× 1) Middle Shekhan Limestone Panoba Reg No L 80216, holotype

Figure 99 *Apolymetis tarkhobiensis* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Middle Shekhan Limestone Tarkhobi Reg No L 80237, holotype

Figure 100 *Apolymetis kohatica* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Lower Shekhan Limestone Shekhan Nala Reg No L 80240, holotype

Figure 101 *Apolymetis kohatica* n sp Ornament of a topotype (× 2) Lower Shekhan Limestone Shekhan Nala Reg No L 80241

Figure 102 *Abra pakistanica* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80245, holotype

Figure 103 *Macrosolen pakistanicus* n sp *a*, dorsal view (× 1), *b*, left valve (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 80248, holotype

Figure 104 *Macrosolen pseudoannuliferus* n sp Left valve (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80249, holotype

Figure 105 *Plagiocardium* (*Schedocardia*) *sparsispinosum* n sp *a*, left valve (× 1), *b*, dorsal view (× 1), *c*, cross-section of ribs (enlarged), *d*, longitudinal section of rib (enlarged) Lower Chocolate Clays Rakhi Nala Reg No L 80256, holotype

Figure 106 *Discors punjabensis* n sp *a*, dorsal view (× 1) (Reg No L 80272, topotype), *b*, right valve (× 1) (Reg No L 80271, holotype) Shales with Alabaster Rakhi Nala

Plate 16

Figure 107 *Trachycardium pseudogigas* n sp *a*, right valve (× 1), *b*, cross-section of ribs (enlarged), *c*, dorsal view (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 80263, holotype.

Figure 108 *Discors nemocardiiformis* n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80279, holotype

Figure 109 *Pitar* (?) *pseudolongior* n sp. *a*, right valve (× 1), *b*, dorsal view (× 1) Shales with Alabaster Rakhi Nala Reg No L 80297, holotype

Figure 110 '*Pitar*' *pseudogastrana* n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Shales with Alabaster Rakhi Nala Reg No L. 80299, holotype

Figure 111 '*Pitar*' *pseudogastrana* n sp *a*, left valve (× 1), *b*, dorsal view (× 1). Lower Chocolate Clays Zinda Pir Reg No L 80428, syntype

Figure 112 *Pitar* (*Calpitaria*) *rakhiensis* n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Lower Chocolate Clays Rakhi Nala Reg No. L 80306, holotype

Figure 113 *Pitar* (*Calpitaria*) *rakhiensis* n sp *a*, dorsal view (× 1), *b*, left valve (× 1), *c*, ornament (enlarged) Lower Chocolate Clays Rakhi Nala Reg No L 80307, topotype

Figure 114 *Pitar* (*Calpitaria*) *rakhiensis* n sp Right valve showing pallial sinus (× 1) Shales with Alabaster Rakhi Nala Reg No L 80314, syntype

Figure 115. *Pitar* (*Calpitaria*) *pseudosubcyrenoides* n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Lower Chocolate Clays Zinda Pir Reg No L 80320, holotype

Figure 116 *Pitar* (*Calpitaria*) *pseudosubcyrenoides* n sp Outline of a right valve (× 1) Lower Chocolate Clays Zinda Pir Reg No L 80321, topotype

Figure 117 *Pitar* (*Calpitaria*) *carteri* (d'Archiac & Haime) *a*, left valve (× 1), *b*, ornament (enlarged), *c*, dorsal view (× 1) Lower Chocolate Clays Rakhi Nala Reg No L 80324, homoeotype

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Figure 118 *Rakhia trapezoidalis* n g et n sp *a*, right valve (× 1), *b*, dorsal view (× 1) Green and Nodular Shales Rakhi Nala Reg No L 80329, holotype

Figure 119 *Venerella parva* n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80330, holotype

Figure 120 *Macrocallista* (*Costacallista*) *punjabensis* n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80341, syntype

Figure 121 *Dosinia rakhiensis* n sp *a*, left valve (× 1), *b*, dorsal view (× 1) Green and Nodular Shales Rakhi Nala Reg No L 80348, holotype

Figure 122 *Solen pseudomanensis* n sp Left valve (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80355, holotype

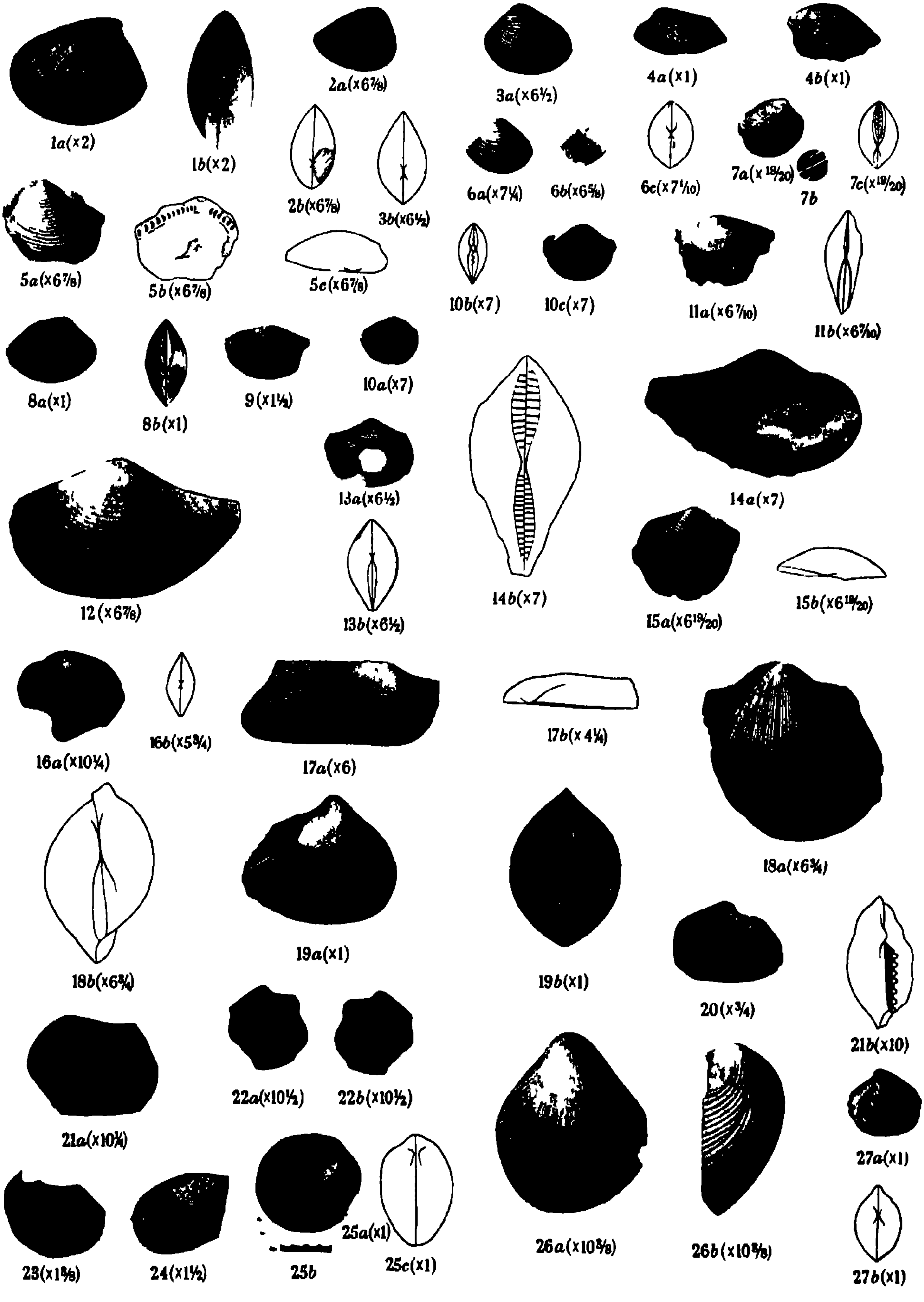
Figure 123 *Solecurtus soriensis* n sp Left valve (× 1) Upper Chocolate Clays Zinda Pir Reg No L 80356, holotype

Figure 124 *Corbula pakistanica* n sp *a*, left valve (× 2), *b*, dorsal view of left valve (× 2) Rubbly Limestones Rakhi Nala Reg No L 80359, holotype

Figure 125 *Corbula* sp A Left valve (× 2) Upper Chocolate Clays Zinda Pir Reg No L 80379, holotype

Figure 126 *Corbula* (*Varicorbula*) *pseudocicer* n sp. *a*, right valve (× 3½), *b*, left valve (× 3), *c*, ornament of left valve (enlarged), *d*, dorsal view (× 3) Upper Chocolate Clays Zinda Pir Reg No L 80391, holotype

Figure 127 *Pholadomya* sp A. *a*, right valve (× 1), *b*, dorsal view (× 1) Shales with Alabaster Rakhi Nala Reg No L 80412, holotype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2*b*(×6⅞)
3*b*(×6½)
6*a*(×7¼)
6*b*(×6⅝)
6*c*(×7¹⁄₁₀)
7*a*(×¹⁹⁄₂₀)
7*b*
7*c*(×¹⁹⁄₂₀)
5*a*(×6⅞)
5*b*(×6⅞)
5*c*(×6⅞)
10*b*(×7)
10*c*(×7)
11*a*(×6⁷⁄₁₀)
11*b*(×6⁷⁄₁₀)
8*a*(×1)
8*b*(×1)
9(×1⅓)
10*a*(×7)
13*a*(×6½)
14*a*(×7)
12(×6⅞)
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26*a*(×10⅝)
26*b*(×10⅝)
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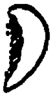
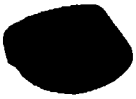
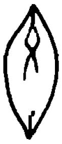
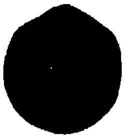

28(×1)


29*a*(×1)

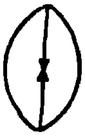
29*b*

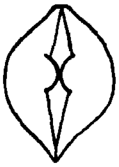

29*c*(×1)

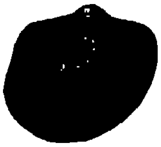
30(×1)

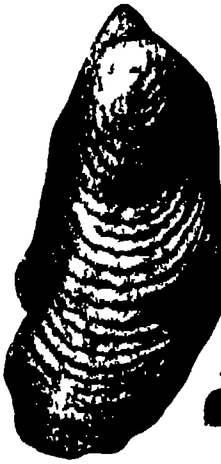

31*a*(×21)

31*b*

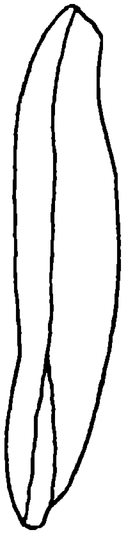

31*c*(×21)

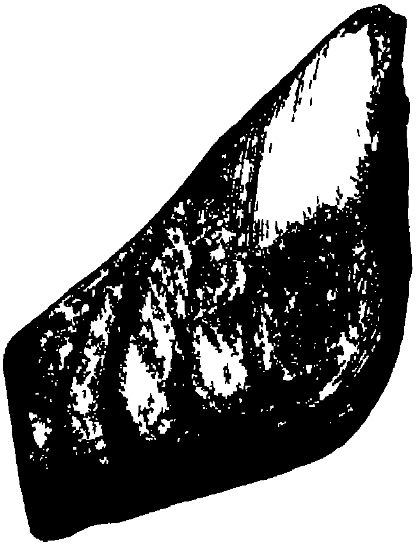

32*b*(×19)


32*a*(×19)


33*a*(×1)

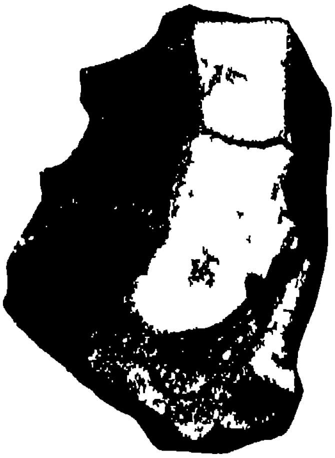
33*b*


34*b*(×½)

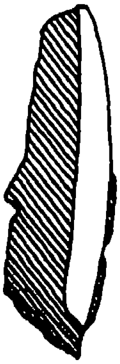

34*a*(×½)

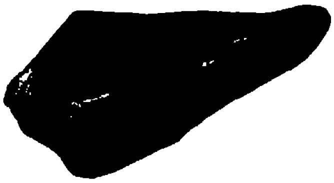
35(×1)

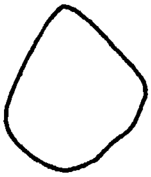
36(×1)


37(×1)

38*a*(×1)

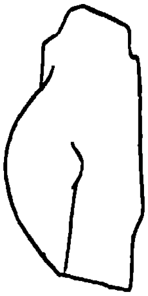

38*b*(×1)

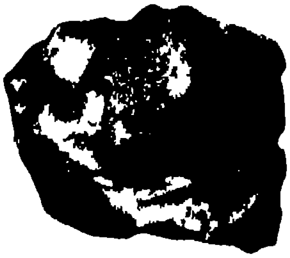

39*a*(×1)


39*b*(×1)

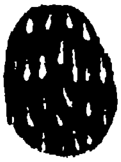
40(×½)

41*b*


41*c*


41*a*(×1)

42*a*(×1)


42*b*

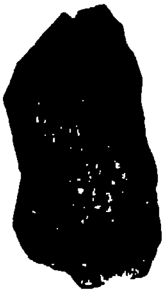
45*c*

45*d*

44*a*(×2)

45*a*(×2)

45*b*(×2)

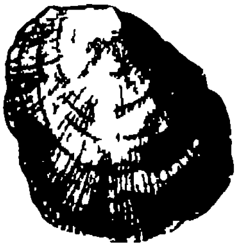

43(×1)

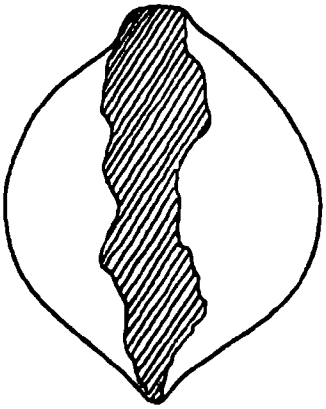
44*b*(×2)

44*c*(×2)

46*a*(×1)

46*b*

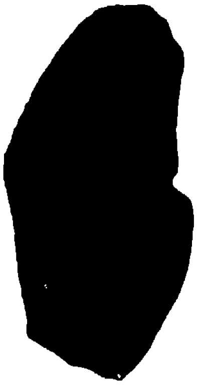

47(×2)

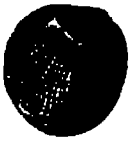

46*c*(×1)

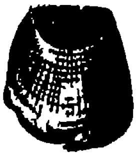
48(×2)

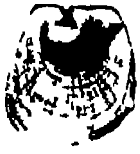
49*b*

49*a*(×2¾)

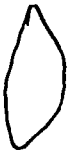

50(×1)

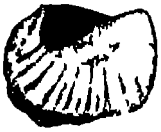

51(×3)

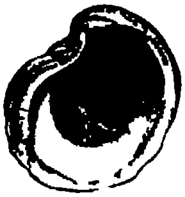

52*a*(×3)

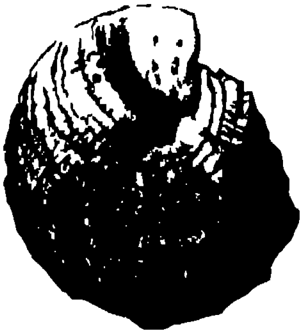

52*b*(×3)

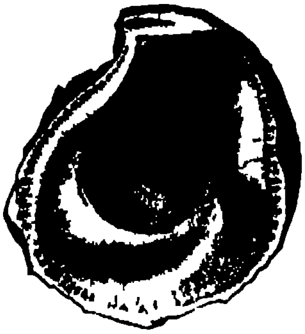
52*c*

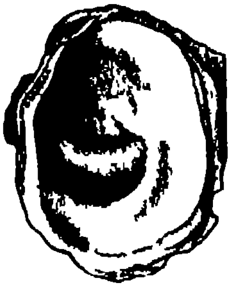

52*d*(×3)

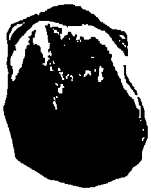

53(×3)

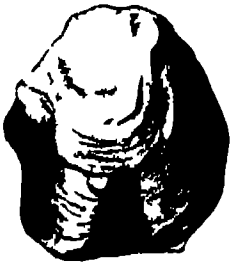

56(×1)

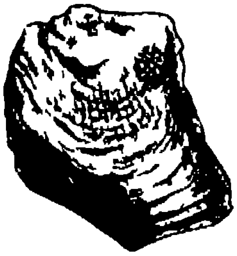

54*a*(×1)

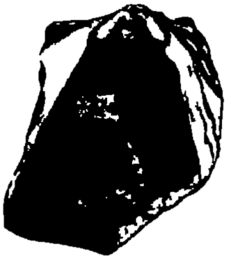

54*b*(×1)

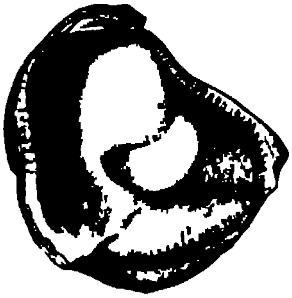

55(×1)

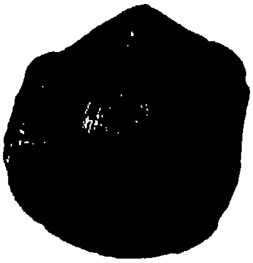

59(×1)

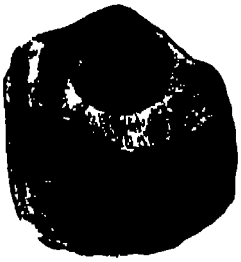

58(×1)


60*a*(×1)

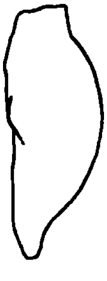

60*b*(×1)

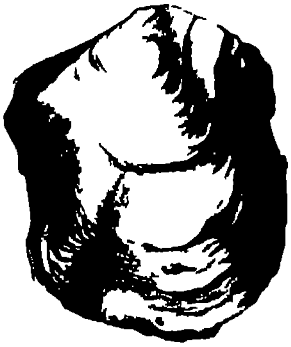

57(×1)

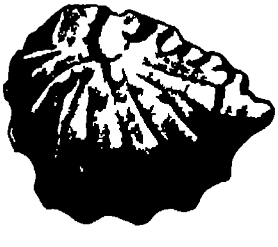

62*a*(×1)

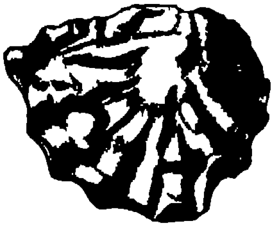

62*b*(×1)

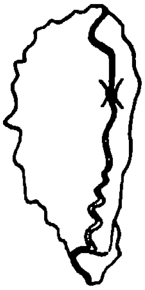
62*c*

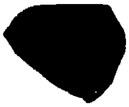

62*d*(×1)

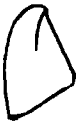

61(×1)

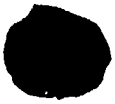

63*a*(×1)

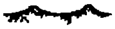

63*b*(×1)

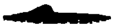

63*c*(×1)

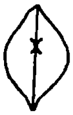

64*a*(×2)

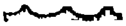

64*b*(×2)

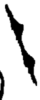

65*a*(×1)

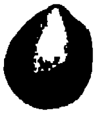

65*b*

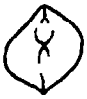

65*c*

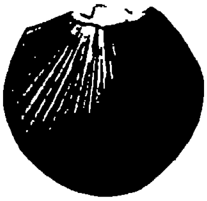

65*d*(×1)

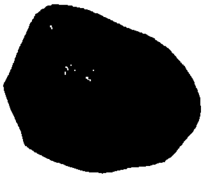

66*b*

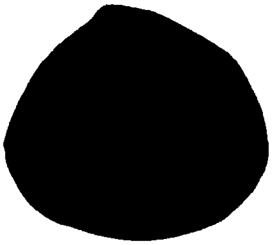

66*c*

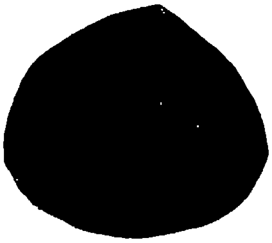

66*a*(×1)

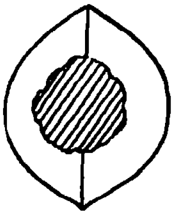

66*d*(×1)

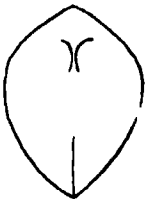

67*a*(×19½)

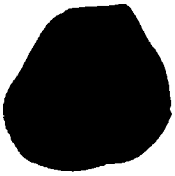

68*a*(×1)

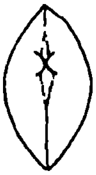

69*a*(×1)

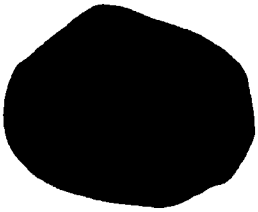

69*b*(×1)

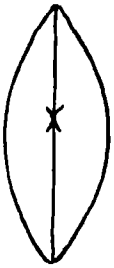

67*b*(×20¾)

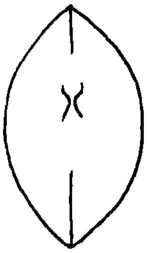

68*b*(×1)

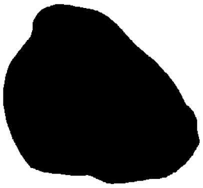

70*a*(×1)

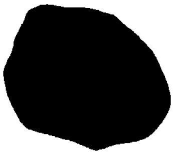

70*b*(×1)

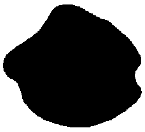

71*a*(×1)

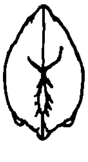

69*c*(×1)

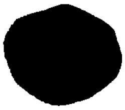

71*b*(×1)

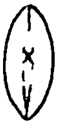

72(×1)

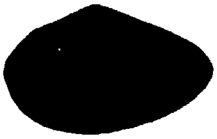

73(×1)

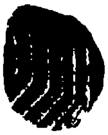

74*a*(×2)

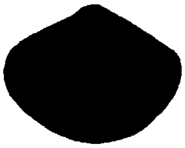

74*b*(×2)

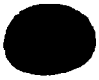

75*a*(×1)

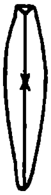

75*b*(×1)

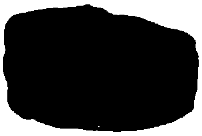

76*a*(×1)

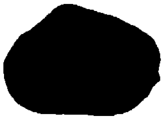

76*b*

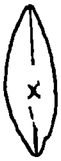

77*a*(×1)

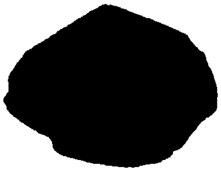

77*b*

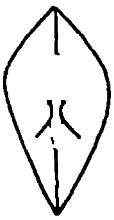

78*a*(×1)

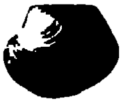

78*b*(×1)


79*a*(×1)

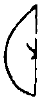

79*b*(×1)


80*a*(×1)

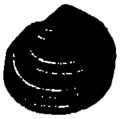

80*b*(×1)



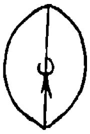
81*a*(×1⅖)



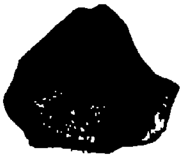
81*b*(×1)



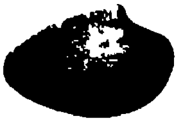
82*a*(×6¼)



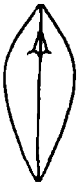
82*b*(×6¾)



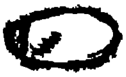
83(×1)



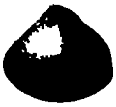
84*a*(×¾)



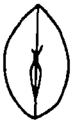
84*b*(×¾)



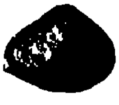
85(×1½)



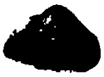
86*a*(×6⅝)



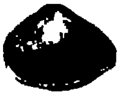
86*b*(×6⅝)



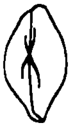
87*a*(×3⅒)



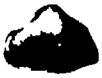
88*a*(×1½)



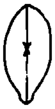
87*b*(×3⅒)



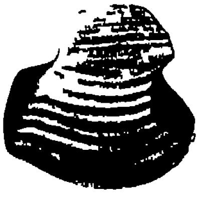
87*c*(×3⅒)



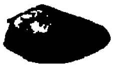
88*b*(×1½)



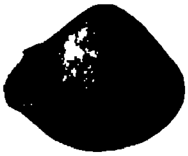
88*c*(×1½)



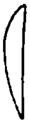
90(×6⅜)



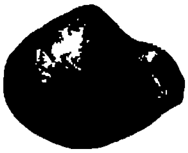
91*a*(×1⅜)



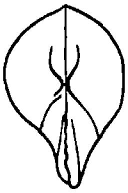
92*a*(×4)



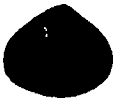
91*b*(×1⅜)



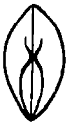
92*b*(×4)



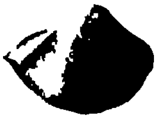
92*c*(×4)



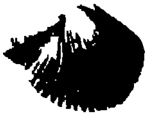
89*a*(×7)



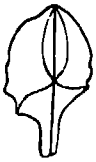
89*c*(×7)



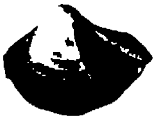
93*a*(×7¼)



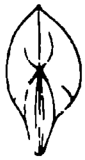
94*a*(×6$^{17}/_{20}$)



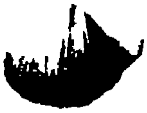
94*c*(×6$^{17}/_{20}$)



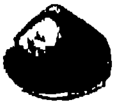
93*b*(×7¼)



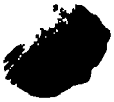
93*c*(×7¼)



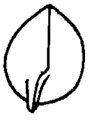
94*b*(×6$^{17}/_{20}$)



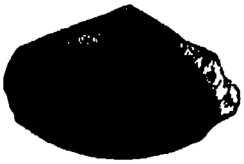
89*b*(×7)



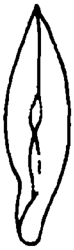
95*a*(×6¼)

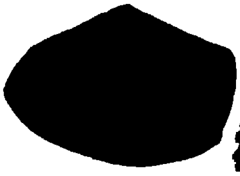


95*b*(×6¼)

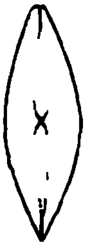

96*a*(×1)

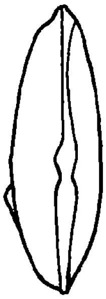
96*b*

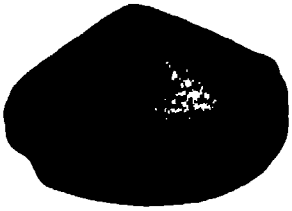

96*c*(×1)

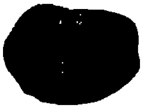

97*a*(×1)

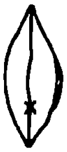
97*b*

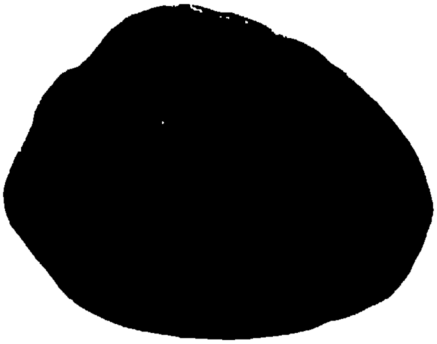

97*c*(×1)

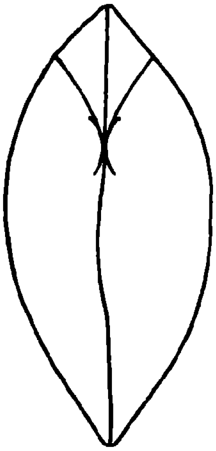

98*a*(×1)

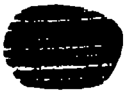

98*b*(×1)


99*a*(×1)

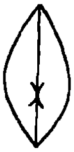

99*b*(×1)

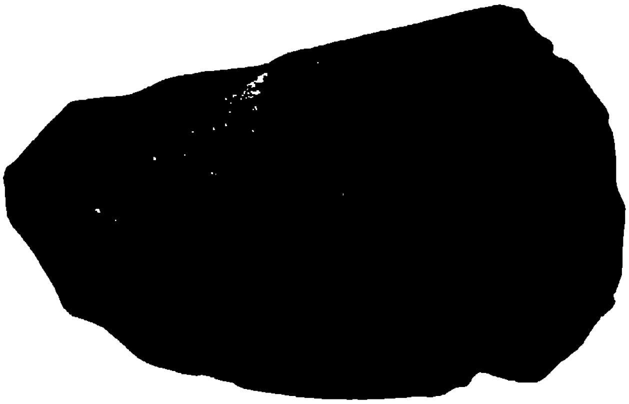

100*a*(×1)


100*b*(×1)

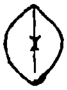

101(×2)

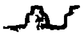
102*a*(×1)

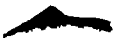

102*b*(×1)

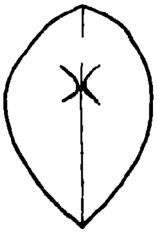

103*b*(×1)

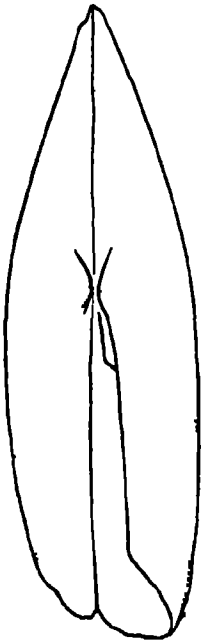
105*a*(×1)


105*b*(×1)

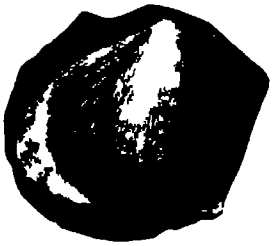

105*c*

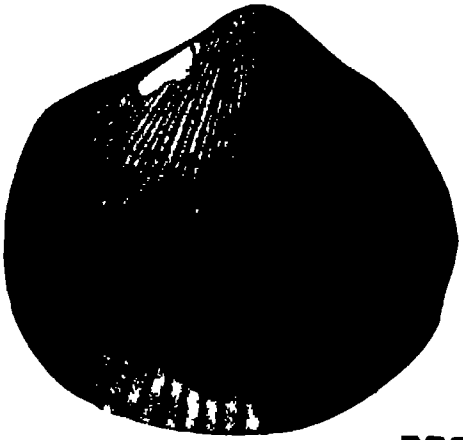

105*d*


106*a*(×1)

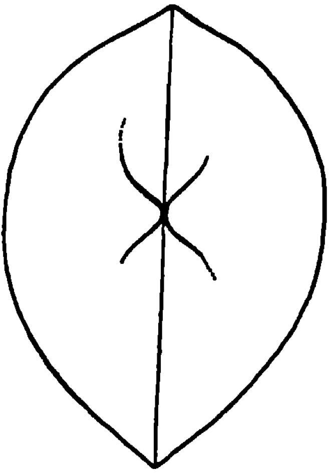

103*a*(×1)

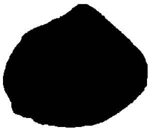
104(×1)

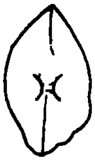

106*b*(×1)

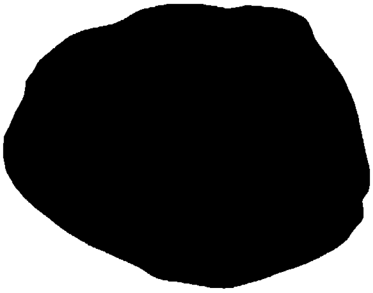

107*a*(×1)

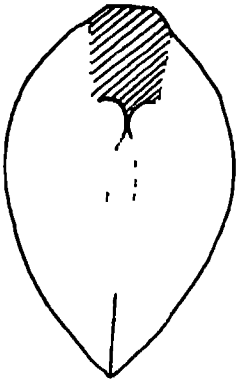
107*b*

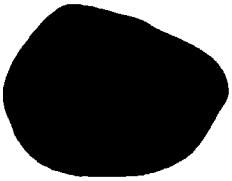

107*c*(×1)

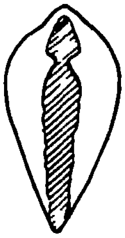

108*a*(×1)

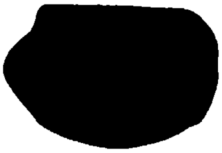

108*b*(×1)


109*a*(×1)


109*b*(×1)


110*a*(×1)


110*b*(×1)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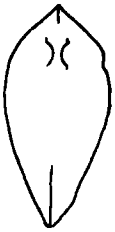
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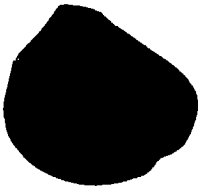
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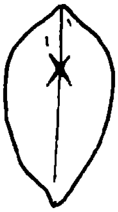
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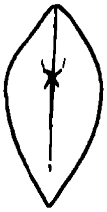
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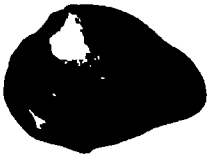
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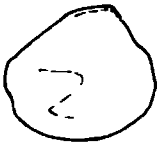
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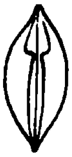
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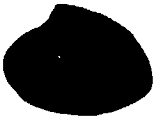
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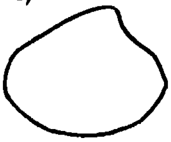
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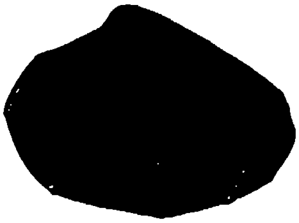
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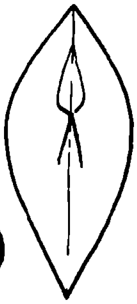
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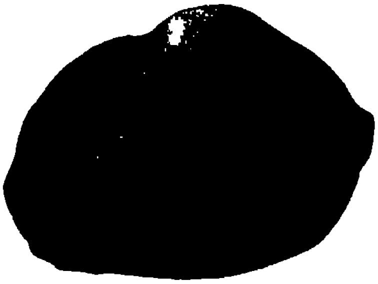

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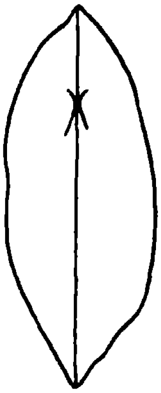

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119*a*(×1)

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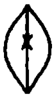

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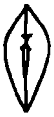

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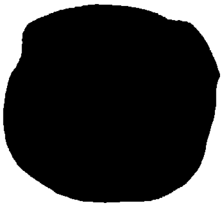

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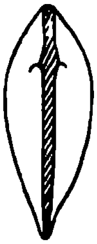

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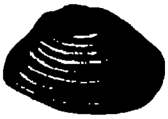
122(×1)

123(×1)



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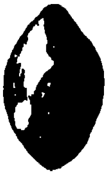

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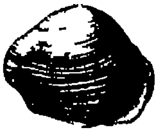
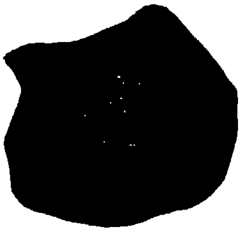


126*a*(×3¼)

125(×2)



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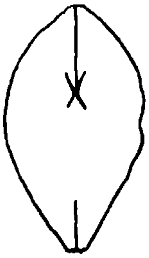

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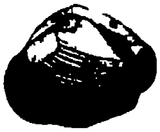

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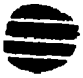
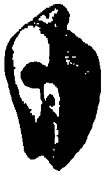


126*c*



126*d*(×3)

THE FRUCTIFICATION OF *CZEKANOWSKIA* AND ITS ALLIES

By T. M. HARRIS, F.R.S., *University of Reading*

(*Received* 16 *January* 1951—*Revised* 20 *March* 1951)

[Plates 18 and 19]

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Leptostrobus cancer n.sp. is described from well-preserved but broken material occurring in the Yorkshire Inferior Oolite (Middle Deltaic). Its fruiting appendages prove to be two-valved capsules, each valve housing a row of small seeds, probably of inverted orientation and with apical archegonia. The new facts have led to a reinterpretation of *Leptostrobus*, and it is now recognized that the Greenland Liassic fossil *Microcheiris enigma* is the same as *Leptostrobus longus*.

Circumstantial evidence is adduced for referring *L. cancer* to *Solenites vimineus* (also called *Czekanowskia murrayana*) and other species of *Leptostrobus* to other species of *Czekanowskia*.

Leptostrobus, as now understood, cannot be placed in any existing family, but for reasons of convenience no new family is at present instituted.

1. Introduction

(a) *General*

Czekanowskia is a well-known genus of Mesozoic leaves; it is widespread, abundant and has a long range, and it has also been closely studied. It is essentially a genus of isolated foliage, and its other organs have remained obscure. However, like nearly all isolated fossil leaves it has been classified, and strong reasons have been advanced for assigning it to the Ginkgoales and this position has been generally accepted for many years.

This paper provides new information about the fossil cone called *Leptostrobus* and reinterprets the previously described specimens. *Leptostrobus* had been already regarded (by myself) as a reproductive organ of *Czekanowskia*, but so far as I am aware, nobody has

Vol. 235. B 628. (Price 8s. 6d.) 63 [Published 18 September 1951

expressed views on my arguments. Further evidence is brought forward here to support this contention *Leptostrobus* is, however, so different from the fructification of *Ginkgo* that it raises grave doubt about the classification of *Czekanowskia* in the Ginkgoales

(*b*) *The* Czekanowskia *group*

A typical member of the *Czekanowskia* group, e g *C rigida* Heer, consists of bundles of long, slender leaves borne on a caducous short-shoot The short-shoot bears small-scale leaves, rather as in *Pinus*, but the foliage leaves are ten or more in number, and are distinguished by forking two or three times The cuticle (known in several species) is similar on the two sides of the leaf Stomata occur in numerous longitudinal rows, the guard-cells are sunken and surrounded by an elongated ring of rather thickened subsidiary cells The venation is seldom visible, but there is evidence that the ultimate branches have sometimes a single vein (Florin gives the number as two), and there are two or even as many as four veins locally below a fork The leaf base, however (which is known from well-preserved, sectioned material), has a single vein which forks below the point of dichotomy of the lamina Florin (1936*a*, p 128) has given a very full account of the structure of this leaf, mentioning all the chief species, and the reader is referred to his account for details

There is unfortunately a difficulty over the name *Czekanowskia* The first member of this group to be described was a Yorkshire fossil for which Phillips (1829) gave a rough sketch and the name '*Flabellaria* (?) *viminea*' There was no description In 1834, Lindley & Hutton gave a slightly better figure and discussed the species at some length, they gave an entirely new name of *Solenites Murrayana*, though they made it clear they were dealing with Phillips's fossil They thought it allied to *Isoetes* It is interesting to note that they prepared its cuticle by maceration, and I believe this is by far the earliest preparation made from a fossil Phillips accepted the change of name without comment in his later work, at that time there was no general acceptance of the rule of priority of nomenclature

According to rule, *Solenites vimineus* (Phillips) would appear to be the correct name of this plant The name *Flabellaria* was preoccupied (by a recent plant), but the specific name is valid because although poorly characterized by the figure there is no doubt about its application, since there is nothing else in the Middle Deltaic flora of Yorkshire to which Phillips's figure could refer

Many years later Heer (1876) described a remarkable series of fossils from Siberia under the new name *Czekanowskia* He did not identify them with *Solenites*, which he considered too ill-characterized, but he compared them Subsequent authors writing on the Yorkshire flora identified *Solenites* with *Czekanowskia*, and as Heer's *Czekanowskia* overshadowed Lindley & Hutton's *Solenites* they used the name *Czekanowskia Murrayana* for the Yorkshire fossil This was the position of Seward who revised it in 1900

I have recently (Harris 1951) redescribed the Yorkshire fossil under what I regard as its valid name, *Solenites vimineus* It proves very close to a typical *Czekanowskia*, the only difference being that in *Czekanowskia* the leaf branches at least twice, while in *Solenites* the leaves are, as far as I know, either simple or only once branched (This branching has been observed in a large number of specimens and is certainly a normal feature, though one easily missed in a leaf over 30 cm long) This difference in branching may hardly be of generic importance, but it seems to me that it is convenient to regard it for the present as a generic distinction and to maintain the familiar name *Czekanowskia* instead of sinking it as a synonym of the unfamiliar *Solenites* In this account, *S vimineus*, or as others name it *Czekanowskia Murrayana*, is regarded as a closely allied plant to *C rigida*, and *Czekanowskia* is treated as a sort of subgenus of *Solenites*

Another genus of this group, *Hartzia*, represented by one species, is only known from the Rhaetic of East Greenland (see Harris 1935, p 42) It is very like *Solenites vimineus* in its general aspect, but the leaf is slightly broader It often forks near its apex, but not in its middle region as in *Solenites* It structure, it agrees closely with *Solenites* and *Czekanowskia*, and if *Czekanowskia* were to be merged in *Solenites* it would be easy to merge *Hartzia* also

It may be noted that Heer identified some peculiar cones and also some rather ill-characterized seeds with *Czekanowskia* This is discussed later

(*c*) Leptostrobus

Heer (1876) described *Leptostrobus* in the same paper as he described *Czekanowskia* *Leptostrobus* is a genus of remarkably slender cones bearing rather distant fertile appendages above and little scale leaves at the base Some of Heer's figures are redrawn in figure 1 and they are further discussed on p 498 No one has ever obtained better specimens of *Leptostrobus*, but Kryshtofovich (1933) figured another good one from Heer's locality Heer's specimens have been compared with *Voltzia* by several authors

The next account of *Leptostrobus* was one by Harris (1935, p 136) on some Greenland specimens which were less perfect than the Siberian ones, but which yielded certain details of structure They were attributed to *Czekanowskia*, but I did not decide whether *Leptostrobus* produced seeds or pollen Later (Harris 1937, p 59) I regarded it as a pollen-producing organ

In the same paper (1935) I described a small seed-bearing fossil as *Microcheiris enigma*, but this I now believe to be the same as *Leptostrobus longus* I also described another fossil as *Staphidiophora secunda* (see figure 1), which I now suggest may be a *Leptostrobus*-like organ of *Hartzia tenuis* The nature of *Staphidiophora* must, however, remain open till fresh material is studied

The only other additions to knowledge of *Leptostrobus* known to me are the discovery by Oishi & Takahasi (1936, p 130), Oishi (1940, p 413), of an imperfect specimen in the Rhaetic of Japan, and another by Turutanova-Ketova (1930) from the Kirghiz

As will be seen, *Leptostrobus* remains a rare and little-known fossil

I am unfortunately very imperfectly acquainted with the Russian literature on palaeobotany published since the beginning of the war, but so far as I know no progress has been made with *Leptostrobus*

The interpretation of *Leptostrobus* in this account is not based, as I would have wished, on one set of specimens supplemented by others but is a structure made by four sets, each by itself inadequate and leaning heavily for support on the others The four sets are Heer's original Siberian cones, the Greenland cones called *Leptostrobus longus*, the Greenland specimen called *Microcheiris enigma*, and the present Yorkshire specimens called *Leptostrobus cancer* I believe I am right in identifying them all generically with one another, but if I am mistaken then a large part of this paper may be groundless The reader's critical attention is directed to this vulnerable point

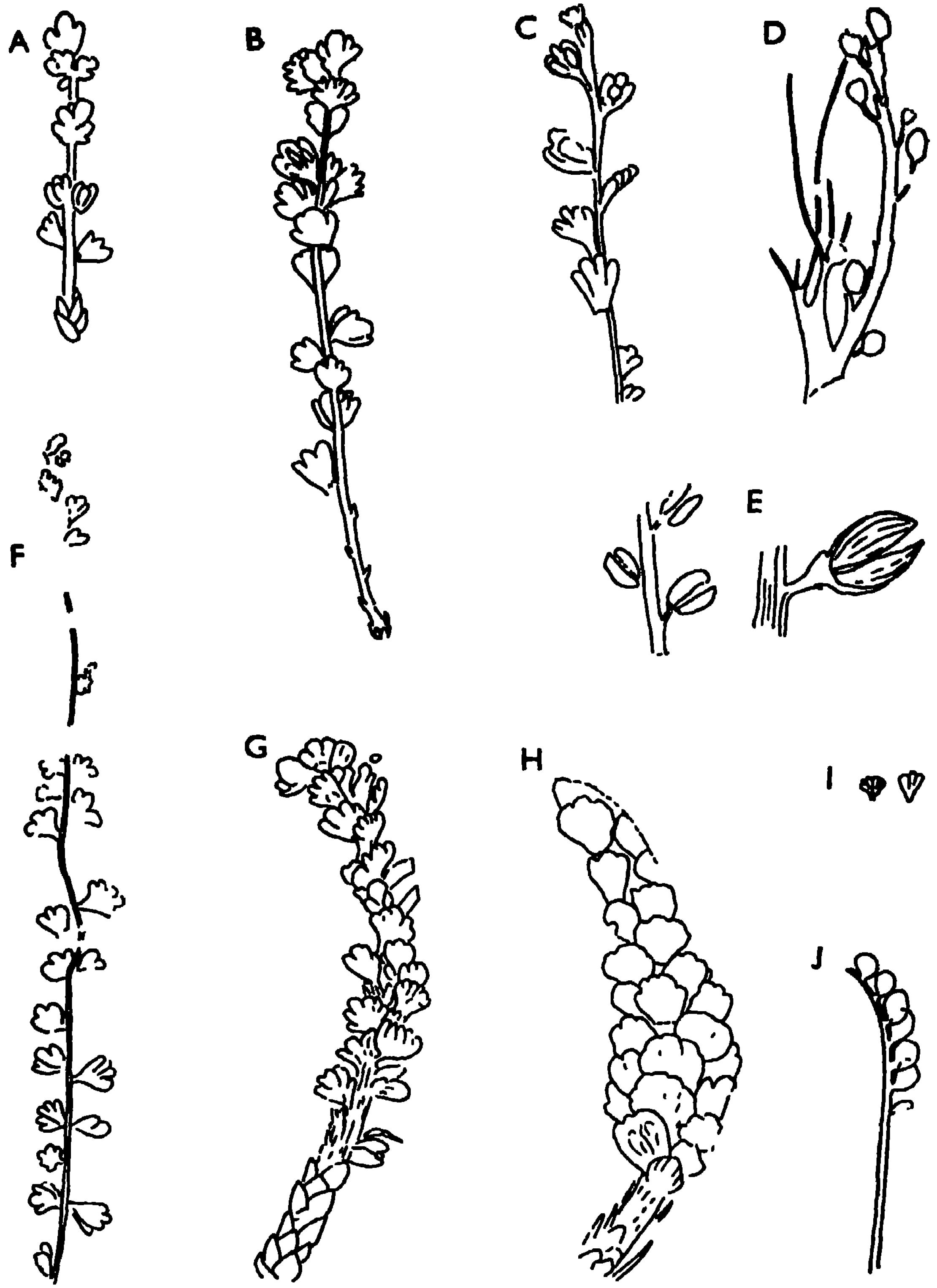

Figure 1 Some fructifications which have been referred to the *Czekanowskia* group The figures are redrawn from the original figures and omit shading and other fine details A–C, *Leptostrobus laxiflora* A, Heer (1880, pl VII, fig 4) B, Heer (1876, pl 13, fig 10A) C, Heer (1876, pl 13, fig 1) D, fructification identified by Heer with *Czekanowskia setacea* Heer (1880, pl VI, fig. 15) E, fructification identified by Heer with *C rigida*, natural size and enlarged, Heer (1876, pl. 21, figs 8A and 8C) F, *Leptostrobus longus* Harris (1935, text-fig. 49A) G, H, *L crassipes* G, Heer (1876, pl 13, fig 14) H, Heer (1880, pl VIII, fig 2) I, the two original specimens of *L microlepis* Heer (1876, pl 13, fig. 15) J, *Staphidiophora secunda*, attributed to *Hartzia tenuis* Harris (1935, text-fig 45A)
)

2 EMENDED DIAGNOSIS OF GENUS *LEPTOSTROBUS* HEER

Seed-bearing fructification consisting of a long and relatively slender axis and small lateral appendages Base of axis covered with small rounded scale leaves Middle and upper parts of axis bearing fertile appendages in a loose spiral Fertile appendage almost sessile, consisting of a somewhat flattened capsule composed of two valves Capsule as a whole rounded or broadly wedge-shaped and attached by the pointed end, distal margin rounded but marked into about five blunt but more or less conspicuous lobes, lobes continued as more or less conspicuous ridges over the face of the capsule

Valves convex outside, probably concave within, margins fitting together, but only joined at the base Seeds about five in number in each valve, one situated under each lobe Seeds oval, inverted (the micropylar end facing the cone axis) and probably possessing a few apical archegonia Seeds possessing a cutinized embryo sac, but no other well-cutinized parts, testa of seed imperfectly cutinized, probably composed of a rather thin layer of fibrous tissue

Cone axis and valves with a well-developed cuticle showing straight-walled cells and numerous stomata Guard cells sunken in a small pit formed by the subsidiary cells Subsidiary cell group elongated on the axis, round or elongated on the valve wall Subsidiary cells often slightly more thickened over their surface than ordinary cells, and with a slight rim of cuticle overhanging the stomatal pit Encircling cells inconstant

3 *LEPTOSTROBUS CANCER* N SP

(*a*) *Diagnosis*

Cone axis (imperfectly known) probably very slender, bearing fruiting capsules at intervals of about 5 mm (Cone base unknown)

Fruiting capsules more or less globose, typically 3 to 5 mm long, 3 to 5 mm broad, valves of capsule with feebly developed lobes, distal margin of capsule typically with three to five very obtuse angles forming the lobes but sometimes evenly rounded Outer surface of valves typically showing three to five broad ridges terminating in the lobes, sometimes evenly convex but substance of valves always with fibrous bands corresponding to the ridges and lobes Inner surface of valve exposed for a distance of 0 5 to 1 0 mm inside the margin, and then meeting the opposite valve

Seeds (? immature) typically 3 to 5 in each valve, elongated, about 2 mm long × 0 75 mm broad (Ripe seeds not known)

Cuticle of cone axis showing straight-walled cells, stomata occasional, agreeing with the more elongated ones of the capsule

Cuticle of capsule wall fairly thick (2 to 3μ measured in folds), of tough consistency Stomata fairly frequent (20 per mm^2), evenly scattered, not forming files or arranged in bands Epidermal cells isodiametric polygons, or slightly elongated in the direction of the capsule margin, mostly arranged in rather ill-marked files running from the base to the margin of the capsule

Lateral walls of cells very strongly marked by a broad, prominent ridge of cuticle, straight but sometimes with very small jagged thickenings Surface wall of cell typically flat, without a papilla, almost smooth but showing an obscurely mottled surface Occasional specimens showing either a large, very ill-defined thickening which forms a vestigial papilla, or with a very ill-defined surface sculpture of longitudinal striations

Stomata well developed, but of rather varied structure Orientation varied, but often longitudinal Guard cells sunken in a pit formed by about five to seven subsidiary cells, pit varying from round to longitudinally elongated Subsidiary cells often forming an

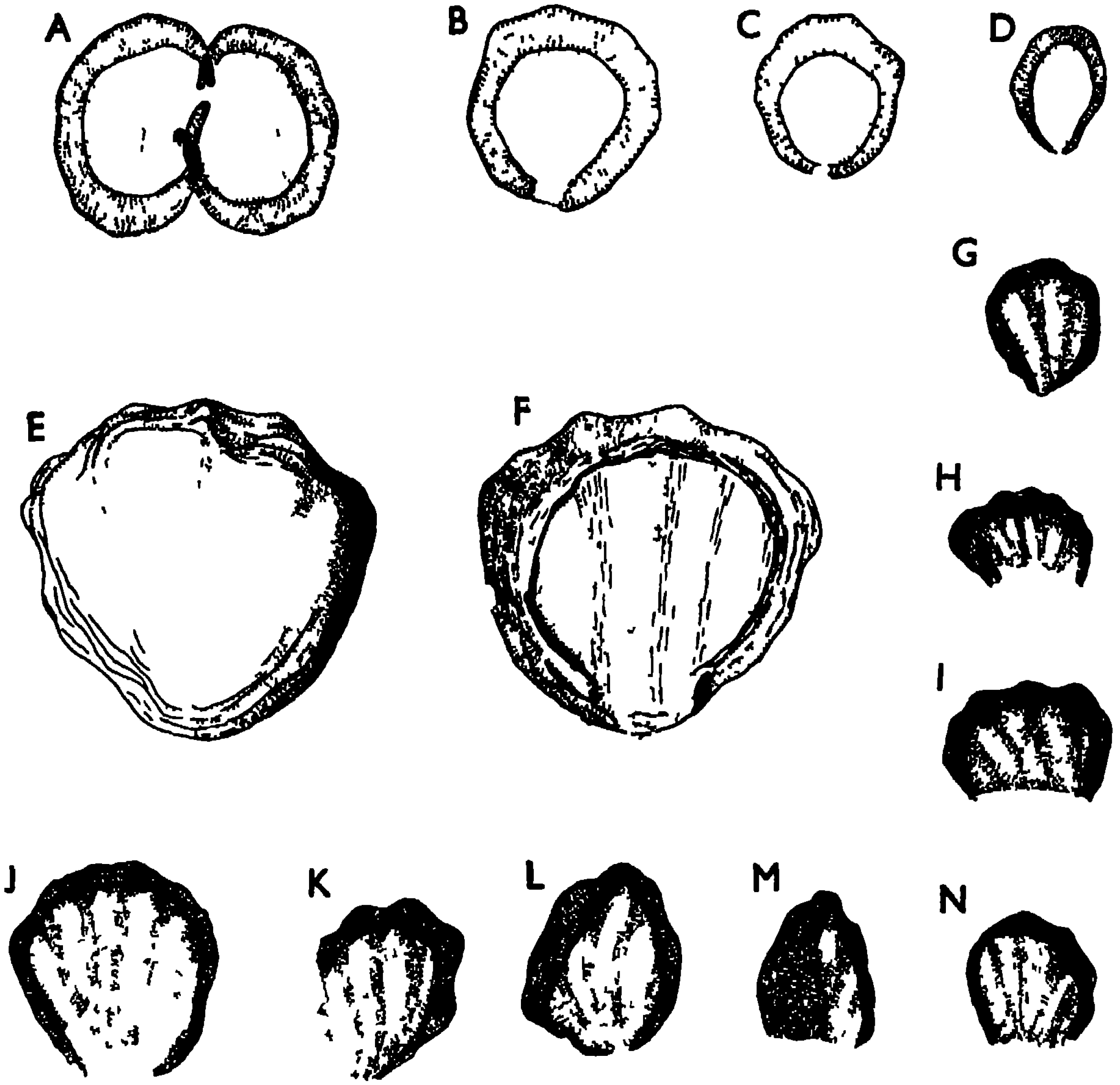

FIGURE 2 *Leptostrobus cancer* capsules A–D, fully macerated cuticles, all at magn ×5, with the infolded margin stippled darker than the valve face A, the two valves of one capsule teased apart, the valve on the left has the thicker cuticle, slide V28564 B, slide V28565, also figured in figure 3G C, slide V28566 D, exceptionally small valve, slide V28567 E, type specimen outside of valve seen as an opaque object, as originally exposed F, inside of same valve in balsam transfer This specimen is also figured in figure 16, plate 18, and figure 23, plate 19, V28568 G–N, series of valves unmacerated or only partly macerated and viewed by transmitted light to show the darker ribs All at magn ×5, slide V28567 The specimen in G is unusually small, those in L and M are exceptional in being obliquely compressed

elongated group, but terminal subsidiary cells undifferentiated or only slightly differentiated Subsidiary cells with slightly thicker surface than the other epidermal cells, usually forming a rim constricting the stomatal pit, pit either round and evenly constricted or elongated and rim better developed at the sides than ends of the pit Encircling cells inconstant, but majority of stomata with some encircling cells, or even with a complete set Exceptional stomata showing two rings of encircling cells Encircling cells usually resembling other epidermal cells in thickness Trichomes absent

The specific name is from *cancer*, a crab, suggested by the resemblance in shape of the isolated valve to an empty shell of a crab (see, for example, figures 2 E, F)

(*b*) *Description*

Material

The material consists of a few blocks of shale collected by me in 1945 from the Cloughton Wyke Solenites Bed (the classic Cloughton locality) and three old blocks in the York Museum, the matrix and flora of two of which almost certainly indicate their origin from the Cloughton Solenites Bed also The third York specimen, preserved in what appears to be typical Gristhorpe Bed matrix, is labelled $\frac{60}{2\,236}$ and mounted on a card labelled 'Middle Estuarine Series, Loc near Scarborough, Sp *Beania* (*Sphaereda*) *parvula*, Bean' It bears three isolated capsules, one of which was macerated

One of the York specimens attributed to Cloughton seems to be the original of Phillips (1829, pl 7, fig 25) This block bears the following labels

Sphaereda parva Bean
Lower Shales Scarborough
Unknown leaves Phillips
Pl 7, fig 25

It has a small red circle denoting a figured specimen

Another label just gives 'W R '

The other York block is labelled 'small vegetable leaves of Phillips, pl 7, fig 25 Lower shale Scarborough'

The name *Sphaereda parva* is, I imagine, a spelling variant of *S parvula*, one of Bean's many *nomina nuda* One York Museum specimen labelled *S parvula* proved quite different, it shows round bodies of the same size as the present capsules which proved to be coprolites full of *Caytonanthus* pollen (Harris 1946)

Both these York specimens and also the ones collected by me show numerous isolated capsules of *Leptostrobus* scattered over one side of the block In my own specimens they are not strictly confined to one bedding plane, but were proved to occur in considerable numbers throughout a thickness of about 5 mm of rock, but none were seen at other levels Some fifty or so capsules are exposed on the rock faces, but most of them are rather damaged About another hundred capsules were obtained by dissolving the rock matrix in hydrofluoric acid, but while most of these again were damaged, either during preservation or in preparation, a fair number of excellent specimens were recovered The cuticle of the capsule is fairly tough and, with care, can be prepared intact

Cone axis

No cone axis is preserved on the surfaces of any of the slabs of rock

When the matrix was macerated, search was made for fragments of cone axes and three such were found All three seem to have rotted a good deal before preservation, and very little internal substance remained enclosed by the cuticle

The largest piece was very crushed and dilapidated, it is 1 cm long and about 2 mm. wide, though its true width is doubtful owing to folds which were torn in preparation It shows three, or possibly four, scars where appendages have been torn off; they occur on all sides, but it is impossible to make out the phyllotaxis

Two other fragments are better preserved and are both just over 1 mm wide One has one scar (figure 25, plate 19) the other has two

The 'scars' consist of an extension of the axis in an outward and forward direction The cuticle is torn in a ragged manner from the axis There is nothing to show whether the appendage was lost before preservation, or broken off during extraction from the rock, but the irregular outline of the cuticle suggests accidental tearing rather than neat abscission

The axis has a cuticle of medium thickness which is tough and easy to handle It is composed of elongated cells with more or less oblique ends The walls are straight and strongly marked, some of them show a slight suggestion of jagged thickenings The surface wall is flat and not papillate, the surface sculpture is of very fine mottling Stomata are rather sparse, between 10 and 20 per mm^2, and some of them seem poorly formed They are scattered (not forming rows) but are all longitudinally orientated The guard cells are sunken, the pit is narrow and formed by an elongated group of subsidiary cells The subsidiary cells are either of just the same thickness as the rest of the epidermis or very slightly thickened, or occasionally slightly thinner They bear no papilla on their surface, but a cutinized rim overhanging the margins of the stomatal pit Encircling cells are variable, sometimes absent, sometimes forming an almost complete ring, but are never specialized

A very few simple trichomes occur on the axis Each consists of a tubular prolongation of the cuticle of an epidermal cell, typically 100 μ long and 25 μ broad

The pieces of axes are identified with the fruits because

(1) they are associated with the fruits,

(2) they are very like the axis of *Leptostrobus longus*,

(3) the scars of the missing lateral appendages are similar in size to the break at the base of the *L cancer* fruits,

(4) the cuticle in general and the stomata in particular are similar but do not resemble those of any other associated plant

The capsules

About half the capsules have their two valves intact, the others are represented by separate valves The valves themselves did not break up before preservation (but were often broken during extraction from the rock)

The capsules shown in plate 18 are of normal size and shape None is appreciably larger than this, but a good many are smaller The smallest seen measured 2 5 mm. long and broad, such specimens are imagined to be starved capsules at the top of the axis.

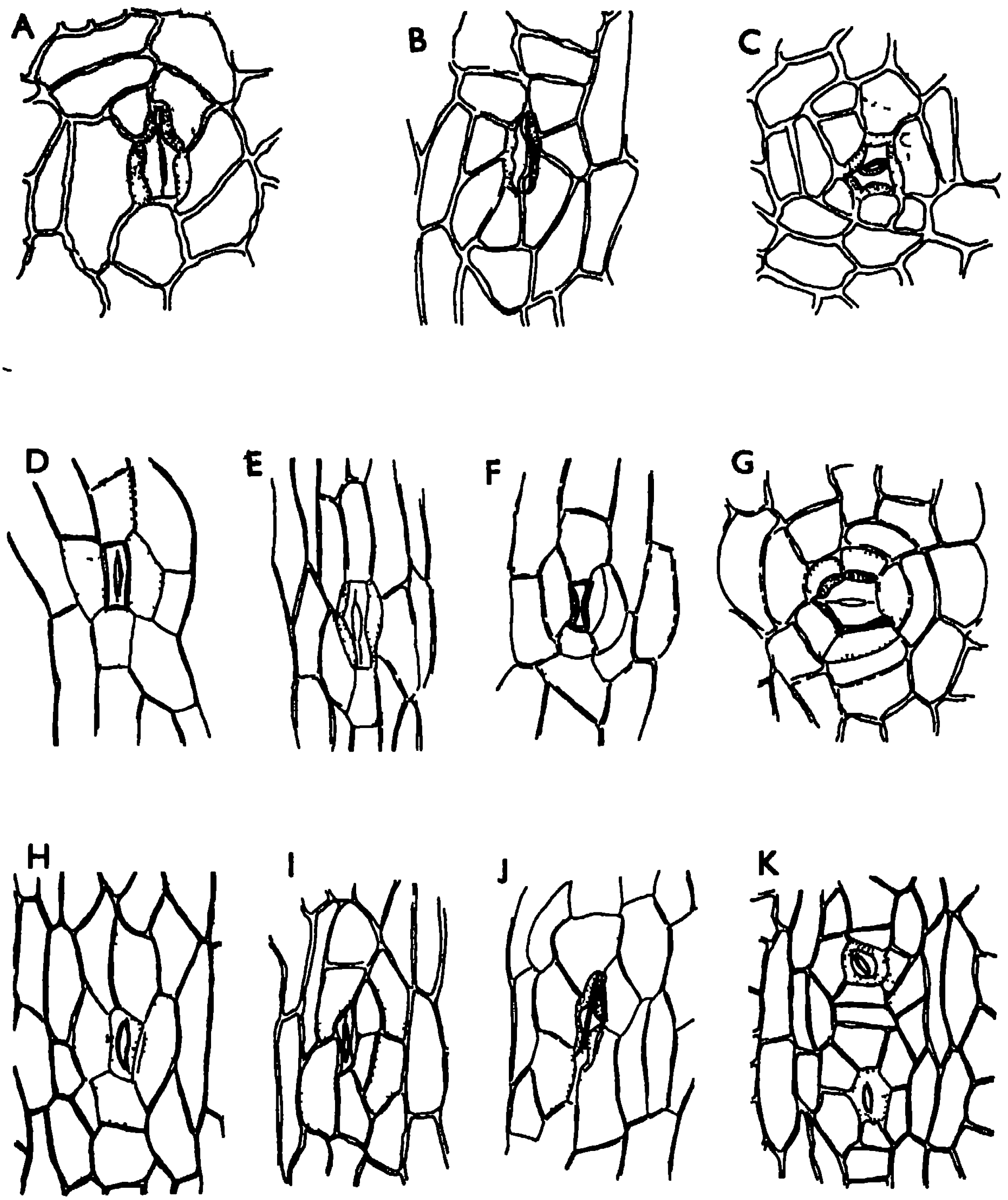

FIGURE 3 Stomata of *Leptostrobus* spp and of *Solenites*, all at magn ×400 A–C, *L. cancer*, three types of stomata from the same valve, all being frequent and within the range of the 'normal', V 28569, also shown in figure 20, plate 19 D, *Leptostrobus longus* typical stoma from valve, Greenland collection slide 2821 E, F, *L cancer*, two stomata on the cuticle of the axis, V 28570 G, *L cancer*, stoma with numerous encircling cells from a specimen in which an unusual number of stomata are of this type, V 28565 (also shown in figure 2B). H–K, stomata of *Solenites vimineus* from specimens associated with *Leptostrobus cancer* H, I, stomata of the commonest type J, exceptional stoma H–J, all from V 28592. K, two stomata, the upper of very unusual type, specimen also figured in figure 27, plate 19, V 28591

Typical valves are about as long as broad, and often nearly round in outline A few are slightly longer than wide, and others slightly wider than long, and there is no reason to suppose that these forms are caused by distortion, but a good many others are distorted and owe their unusual shapes to unusual planes of compression Such specimens suggest that the valve was a little flatter than hemispherical, making the whole capsule nearly globose Where the two valves are still present they usually fit together (figures 11 and 17, plate 18) but not closely enough to exclude rock matrix, the specimen shown in figure 12, plate 18 where they diverge is exceptional

The capsule illustrated in figure 2A shows a difference in thickness between the cuticles of the two valves, though their cells are similar Other specimens may also show such a difference, but this is less marked

The figured specimens illustrate the variation in the shape of the valve margin The commonest form is one where the distal margin has three to five obtuse angles Specimens in which the 'angles' are extended to form distinct bulges are common and also some where the angles are almost suppressed so as to give an evenly rounded outline to the valve

The surface of the valve usually shows a series of obscure broad ribs running to the marginal 'angles', these ribs too are variably developed and occasionally are obscure Even where the surface is smooth the position of the rib is often made obvious by colour, the rib being thicker and black, the intervening space thinner and brown The only specimens showing no sign of the ribs are those which have suffered complete natural (or artificial) maceration and nothing but cuticle remains Specimens which have suffered a moderate amount of natural maceration often show the distal end of each rib as a conspicuous dark patch, when the rest of the rib has disappeared

Specimens compressed in unusual planes suggest that the ribs were originally much more prominent than they are in the compressed fossil The presence of little compression folds in the cuticle along the sides of the ribs points the same way

The substance of the wall of the valve is just thin enough to transmit light in the best specimens In the better specimens the valve seems to be lined with a hypodermis of cells about 40 × 40 μ There are oval gaps in this layer, probably above each stoma This layer is supplemented (or possibly replaced) by elongated cells along the ribs, it was not possible to make out the ends of these elongated cells, but they suggest fibres At a rather deeper level there is an incomplete layer of large oval cells 50 × 60 μ which are evenly scattered in the areas between the ribs Their walls are thick, and they are regarded as sclerids or isolated stone cells

No other cell layers are recognizable in the unmacerated valve, but it is possible that there were a good many layers of delicate cells forming a soft tissue

The base of the valve is irregularly broken and often shows a large gap In the best specimens the outer surface of the valve is almost unbroken, but a piece of the marginal flange is missing As a rule there is an irregular tear at the base of the outer wall of the valve as well

Marginal flange

The marginal flange is the part of the valve which faces the opposite valve in the intact capsule The flange is typically about 0 6 mm wide in the distal region and grows narrower, about 0 3 mm wide near the base At the base it is always broken away The substance of the margin appears to be a little less massive than the rest of the valve wall, and the fibrous layer of the ribs may not continue into it, it was, however, difficult to obtain evidence, as much of the marginal flange is fused to the rest of the valve Near the free edge of the flange the substance suddenly becomes delicate

The angles or lobes of the margin were carefully examined to see if there was any kind of opening here There is not, on the contrary, the cuticle is slightly better developed here than elsewhere

The seed

The seed of *L cancer* is ill known, very few of the capsules show any trace of seed, and even these may be unripe or abortive specimens

Figures 5 to 8, plate 18, show two valves in which pieces of the chalazal ends of seed are present, though much has been broken away, probably in preparation Each seed is connected by a dark strand to the tissue beneath a lobe of the capsule, and each seed shows a dark inner mass (the megaspore membrane) surrounded by an integument-like layer which on maceration proves to be the 'fibrous membrane' described below

A few capsules are closed and contain no rock matrix, and these always show many seeds, but they are so delicate that they are usually broken in small pieces In figure 26, plate 19, the dark matter behind the margin proved, under different lighting, to consist largely of the chalazal ends of megaspores, while the less dark part below this is chiefly broken pieces of the 'fibrous membrane' Figure 10, plate 18, shows a nearly intact but very small megaspore membrane dissected out of such a capsule, as a rule the megaspore membranes seem to be 1 0 to 1·5 mm long

The specimen in figure 26, plate 19, is not quite fully macerated It is unusual in that all its megaspore membranes are of small size, well under 1 mm long Below some, and perhaps all, of the megaspores there is a small dark nodule very like the pollen masses of the specimen called *Microcheiris* Accordingly, it was removed and further macerated, and it was proved that each was in fact a pollen mass One of these masses teased out from the capsule is shown in figure 24, plate 19, and in figure 4B, the others are similar or a little larger, but the pollen grains composing these masses are so numerous and so compacted together that it is not possible to trace the outline of any one of them completely

The innermost layer of the capsule which is called the fibrous membrane proved troublesome to investigate and is by no means understood After maceration it consists of a soft material showing very dimly the outlines of several layers of cells The fibrous membrane forms a sheath round the chalazal ends of the seeds just as an integument would do, but it also extends far beyond the apices of the embryo sacs down to near the base of the capsule, as though it here forms the inner lining of the capsule The scattered pollen grains in the capsule are all sticking to this layer

It is supposed that the fibrous membrane represents several layers of cells which have been preserved because of a slight fat impregnation It is certainly associated with the seeds because most of the capsules have lost their seeds and have lost their 'fibrous membranes' also, but its position and nature is left open

The megaspore membranes of *Leptostrobus cancer* vary in size, but are nearly constant in fine structure They were repeatedly proved to be a double membrane (a collapsed sac) and the two surfaces, though very close, are not fused together, so there must be a little soluble matter between them There is some variation in different parts of a single megaspore in the folding of the surface and in the density of granules, that in figure 9, plate 18, shows conspicuous folds and few and therefore distinct granules The folds sometimes look just like cell outlines, but often they cross one another, and it seems likely that none of them are true cells

After archegonium-like cavities had been found in the apices of the megaspores o '*Microcheiris*' a search was made for similar ones in the megaspore fragments in *Leptostrobus cancer* No convincing example was found, but the occurrence of pollen masses in the specimen shown in figure 26, plate 19, in the same position as those of '*Microcheiris*' indicates that the seeds are inverted here also

It is unfortunate that the seeds are so imperfectly known The rock matrix was searched for isolated seeds of suitable structure but none was found

Pollen grains in the capsules

None of the present specimens is as richly provided with pollen grains as the Greenland ones (especially '*Microcheiris*'), but all those that still possess the fibrous inner membrane show moderate numbers of grains scattered over it The specimen shown in figure 26 has, in addition, several compact masses of pollen situated just below the embryo sacs, in positions which correspond with those of '*Microcheiris*', and there are similar pollen masses among the broken fragments from inside other specimens It is very difficult to make out the form of the pollen grains in these masses as they overlap, the only thing certain is that there are many large grains, some about 50 μ wide, with rather thin, very finely punctate walls I am not able to say whether wings and triradiate scars are absent, but I could see none

Around these pollen masses there are scattered pollen grains which can be observed better, some of these are large oval grains up to 80 × 50 μ with longitudinal groove, and others roundish grains about 35 μ wide, also with a longitudinal groove I did not recognize any winged pollen grains at all, but I saw a few thick-walled grains looking like fern spores

I feel certain that these pollen grains are of more than one species In the Greenland specimens there was much greater variety in pollen, including at least the following four kinds, all of them abundant

large winged grains	130 μ × 80 μ
large oval grains	90 μ × 60 μ
smaller oval grains	35 μ × 30 μ
round grains	30 μ diameter

In view of this variety one would hesitate to suggest that any particular kind belonged to *Leptostrobus* Clearly, however, the probable absence of winged grains in *L cancer* is rather against my former idea that the winged pollen belonged to it

(*c*) *Comparison of* Leptostrobus cancer *with other species of* Leptostrobus

The other named species of *Leptostrobus* (cones) are *L laxiflora*, *L crassipes* and *L microlepis* from Siberia and Russia, *L longus* from east Greenland, and there is an unnamed specimen resembling *L. longus* from Japan. Of these, *L microlepis* is too ill-known for comparison, it might be an ill-developed *L laxiflora*, Kryshtofovich & Prinada (1934) omit it from their list

L cancer has a slender axis like *L laxiflora* and *L longus*, but both of those species differ in their strongly lobed capsules *L crassipes* (with a thick axis) has capsules which agree in their feebly developed lobes and surface ridges, but they are usually much larger

L longus, the only other species whose structure is known, has a very similar cuticle indeed The cuticle of the axis of the two species is at present indistinguishable, it is true that no trichomes are known on the axis of *L longus*, but they are so rare in *L cancer* that they can hardly be used as a distinguishing character The cuticles of the capsules, though very similar are, however, distinguishable, *L cancer* has as a rule smaller, thicker walled cells (30 to 40 × 25 μ) than *L longus* (70 to 80 × 40 to 50 μ) In *L longus* the stomatal apparatus of the capsule nearly always has an elongated pit, but in *L cancer* it is very often rounded

The inner (fibrous) membranes of the capsules in the two species, and their megaspore membranes, are at present indistinguishable

4 REVISED DESCRIPTIONS OF ALLIED SPECIMENS

(*a*) *The Greenland specimens called* Leptostrobus longus

(Harris 1935, p 138, pl 7, figs 1–5, 11–17, ? figs 6–10, ? pl 24,
fig 8, text-fig 49, text-fig 50 I)

I have not examined the hand-specimens again They were only indifferently preserved, and were made rather worse through my efforts to work out their structure by maceration They are in the collection of the Geological Survey of Greenland at Copenhagen

I have, however, re-examined all the preparations of cuticles, and while I can confirm most of what I previously stated, certain facts are now recognized for the first time and my account is corrected I had supposed that the lateral organs were originally cup-shaped This was a mistake, one of the preparations (2881) shows the lateral edge of a valve though this feature was missed Accordingly, a new restoration is given here

The inner membrane of the capsule wall was barely mentioned, but search showed a few fragments of a layer agreeing with the peculiar 'fibrous membrane' of *L cancer* Various kinds of pollen grain occur sticking to this membrane

(*b*) *The Greenland specimen called* Microcheiris enigma

(Harris 1935, p 118, pl 8, figs 5–6)

This specimen is important because it gives the best picture of the valve of *Leptostrobus longus* and because it shows certain features even better than *L cancer*

The single specimen was obtained by maceration of shale and was fully cleared when found. It is re-illustrated here because, being now better understood, it can be followed more closely

The specimen is a small scale or valve nearly 6 mm long × 5 mm broad Its base is broken and the top is divided into five blunt 'fingers' As mounted, it consists of cuticle only, and has been severely crushed in preservation, the cuticle shows many compression folds round the margins and elsewhere

The cuticle of the outer side continues over the lateral margins and around and over the fingers and then changes abruptly on the inner side at a distance of about 1 mm from the distal margin and becomes very delicate and is largely missing This delicate extension overlaps the distal ends of the seed megaspores Apart from this, no cuticle remains over the seed megaspores, but comparison with *L cancer* suggests that the 'fibrous membrane' occurred here but was lost in preparation

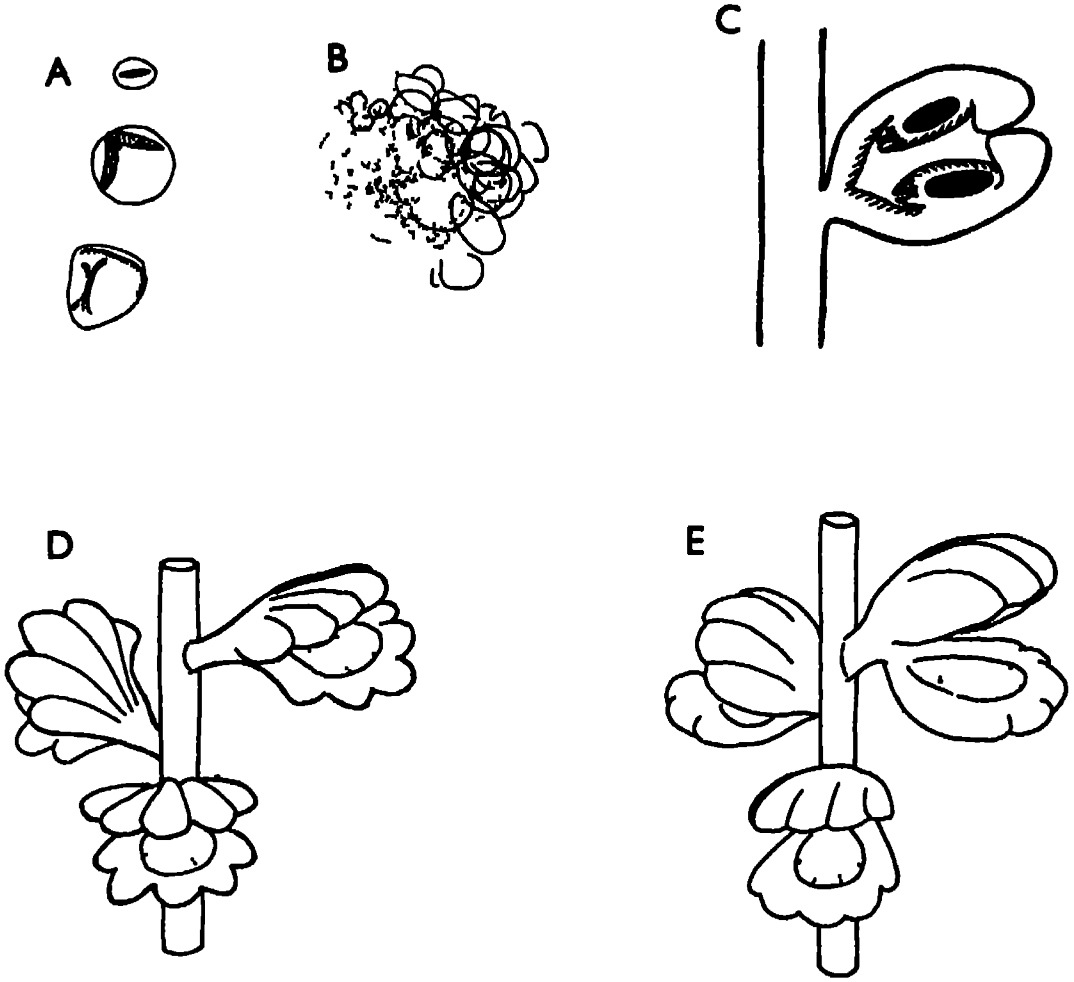

Figure 4 A, three pollen grains or spores of unknown origin adhering to the inner cuticle of a capsule, V 28580 (Magn × 200) B, pollen mass dissected from below a seed megaspore Only the more obvious grains are indicated, the stippled matter shows no distinct structure (shown also in figure 24, plate 19 V 28578 (Magn × 100) C, restoration of *Leptostrobus* capsule in L S The megaspore is shown in solid black, the inner fibrous cuticle is cross shaded and the pollen grains are shown as black dots The micropyle of the seed is entirely imaginary (Magn × about 5) D, restoration of part of a *Leptostrobus longus* cone (Magn × about 5) E, corresponding restoration of part of a *L cancer* cone (Magn × about 5) In D and E the morphological apex of the cone is shown upwards

The rest of the inner face of the fossil is covered with a very delicate and fragile membrane (the fibrous membrane) which has a considerable affinity for stain It has cracked into little rectangular blocks, many of which are missing It shows no clear cells at all, but only faint and obscure striations suggesting a mass of crushed fibres rather than an epidermis

The relations of this delicate fibrous layer to the cuticle at the margin of the valve could not be made out.

There is an embryo sac below each 'finger' or 'lobe' These sacs are crushed flat, but the upper and lower sides can be recognized as non-cellular membranes covered with small granules which are irregularly united into irregular lumps Nothing remains inside the embryo sacs

The apex of each embryo sac points towards the base of the scale and is emarginate, as though either strongly depressed, or else slightly torn at this point before preservation In addition, four of them, and perhaps the fifth also, show a small round gap at this end about 40 μ wide which I interpret as the opening for an archegonium neck, one of them gives an indication of a second of these gaps No such gaps occur in any other part of the embryo sac

Above the chalaza of each embryo sac there is a faint and ill-defined dark patch, due to a little darkly stained matter in this region, but this matter reveals no definite cells, but only very obscure striations

The inner cuticle of the valve is thickly covered with pollen grains though these are of several types, and their distribution is very uneven In the distal region they are very few indeed, barely as many as 1 per mm ^{2}, and there are probably none at all sticking to the cuticle of the outside of the valve They become numerous, however, on the inner sides of the base of the valve where the number reaches about 60 per mm ^{2}, and the concentration increases on the inner face of the valve below the bases of the seeds where the grains are more or less in contact or overlap Finally, at a point 0 3 mm below each seed there is a solid compact mass of pollen, each mass consisting of perhaps 100 pollen grains No tissue is preserved connecting these pollen masses with the embryo sacs, but there is a suggestion of a core in each pollen mass and there is also a suggestion that the pollen masses are not quite shapeless but slightly moulded into a cone These masses must owe their existence to some original structure in the valve, and while it may be imagined that the pollen is situated at the bottom of a micropyle in a nucellar pollen chamber, there is no trace of these parts

It was noticed that a few pollen grains occur beneath the edges of the embryo sacs, especially in their apical regions, and this seems to show that there was originally a gap between whatever tissue surrounded them and the wall of the valve, but this gap did not extend far

In my account I regarded *Microcheiris enigma* as a flattened, seed-producing organ, as indeed I do now, and I regarded the capsule of *Leptostrobus longus* as a radially symmetrical organ of entirely different nature I did not discuss their identity It was only when *L cancer* was investigated, a fossil which showed obvious resemblances to each, that the possibility was first considered, it was then confirmed by re-examination

'*Microcheiris*' is the same size as the 'cup' of *Leptostrobus longus* and is divided very similarly into lobes Its axis is unknown, but the cuticle of the valve can be compared That of '*Microcheiris*' is slightly more delicate and is somewhat shrivelled, showing many small folds which are not original since they cross cells irregularly The epidermal cells themselves are identically similar A feature which was missed in '*Microcheiris*' is that the cuticle continues over the margin and then abruptly ends (or becomes very delicate) just as in *Leptostrobus longus* (and in *L cancer*)

Stomata are difficult to find on the valve of *Microcheiris* and were reported absent The specimen is mounted with the inner side upwards, and in any case the cuticle is much folded Search has, however, revealed some stomata, their subsidiary cells are like those of *Leptostrobus longus* but less thickly cutinized

I think the difference may be all due to immaturity of '*Microcheiris*' which would account for the presence of young seeds, thinner cuticle and wrinkled surface The specimens called *Leptostrobus longus* are full grown and empty husks

The generic identification of '*Microcheiris*' with *Leptostrobus cancer* is based on strong evidence Besides the general agreement in shape with *L cancer* valve we have agreement in the extent of the outer cuticle of the valve (extending over the lobes and then stopping abruptly), agreement in the very remarkable inner cuticle of the valve, agreement in size and character of the megaspore membranes, agreement in the position of the pollen masses

The value of '*Microcheiris*' is in the light it throws on the other specimens of *Leptostrobus longus* and in the information it gives about the number and position of the seed megaspores, and their associated pollen masses

(*c*) *The specimen called* Staphidiophora secunda

(see Harris 1935, p 114, pl 8, figs 3, 4, 9, 10, 11, text-fig 45)

A single specimen of this fructification was found associated with *Hartzia tenuis*, and was identified with it because it has similar stomata The specimen is redrawn in figure 1, it is seen to be rather like *Leptostrobus* except in the secund arrangement of the appendages, but this results from twisting of the axis

The appendages were macerated and yielded the cuticle fragments I described, and it was concluded that the lateral appendages were seeds This interpretation is possibly correct, but an alternative which is now realized to be possible is that the appendages are capsules containing a number of small seeds This can only be settled by the study of further specimens, but it is clear that just as the leaf *Hartzia* agrees closely with *Solenites*, the fruits attributed to the two may be closely similar

The small fossil described by me as *Staphidiophora* (?) *exile* (Harris 1935, p 116) is too little known to be discussed here

(*d*) *Notes on Heer's Siberian specimens of* Leptostrobus *and the fructifications attributed to* Czekanowskia

(*Leptostrobus laxiflora* Heer 1876, p 72, pl XIII, figs 10–13, pl XV, fig 96,
Heer 1880, p 23, pl VII, figs 1–5)

Heer's figures (see figures 1A to C in this paper) represent excellent specimens which may well form a true species, but their botanical nature is obscure The drawings suggest a variety of different seed arrangements, and I would suggest that bodies he regarded as seeds are true seeds but are seen as bulges through the capsule wall

Leptostrobus crassipes Heer may be divisible into two groups, one with 'scales' or capsules the same size as in *L laxiflora* (Heer 1876, pl XIII, fig 14, 1880, pl VII, fig 7, pl VIII, figs 4, 5), the other has larger 'scales' with an entire margin (pl VIII, figs 2, 3). One specimen (1880, pl VIII, fig 1) links the two groups A point of considerable interest is that in his 1880, pl. VIII, figs 2 and 3, the 'scales' imbricate in a phyllotactic spiral This indicates that they are approximately in their true position and are vertically flattened as Heer supposed, and if they are composed of two valves, then one valve is above the other

Leptostrobus microlepis Heer, 1876, p 74, pl XIII, fig 15, 15*b*, 15*c*, 1880, p 25, pl VII, fig 6, is ill-characterized and may be the apical part of *L laxiflora*

Leptostrobus rigida Heer, 1880, p 25, pl VII, figs 11, 12, pl VIII, figs 1*b*, 5*b*, and *L angustifolia* Heer, 1880, p 26, pl VII, figs 8–10, are the names of elongated leaves in bundles, rather closely resembling *Solenites vimineus*

Fructification attributed to Czekanowskia rigida (see Heer 1876, pl XXI, fig 8, redrawn in figure 1E) This fossil looks as though it may possibly be of *Leptostrobus* nature, but it could equally well be an axis bearing paired seeds as Heer supposed Its reference to *Czekanowskia* seems to be suggested by its *Ginkgo*-like appearance

Fructification attributed to Czekanowskia setacea (see Heer 1880, pl VI, fig 15, redrawn in figure 1D) I think it unlikely that this fossil belongs to *Czekanowskia* at all, as the leaf-like appendages are so differently attached

5 EVIDENCE OF ATTRIBUTION OF *LEPTOSTROBUS* TO *CZEKANOWSKIA*

The evidence of attribution is

(1) association, repeated for several localities and different species of different ages,
(2) agreement in structure

General position

It is curious that Heer never discussed the possibility that *Leptostrobus* might belong to *Czekanowskia*, he decided that *Leptostrobus* was a *Voltzia*-like conifer while *Czekanowskia* was the foliage of a *Ginkgo* ally, and this being so they could have nothing to do with one another The fact that *Leptostrobus* bears little leaves at its base, looking very like the foliage leaves of many conifers, was part of Heer's evidence These scale leaves might, however, have been taken as evidence that *Leptostrobus* does not belong to a plant with shoots bearing such scale-like leaves, since no such conifer occurs with them

In a later paper he regarded some narrow pine-like leaves as the foliage of *Leptostrobus*, and in view of their resemblance to *Solenites* he may well have been right Later authors endorsed Heer's view that *Leptostrobus* is allied to *Voltzia*, and as far as I know the first expression of another view was my opinion (1935) that it belonged to *Czekanowskia* *Czekanowskia* and *Leptostrobus* are associated on many of Heer's figured blocks, but he selected some other fossils as fructifications

Association

Association between fossils proves only one thing that they were more or less associated during life, occurring at the same time and in the same district It is chiefly when such association is repeated that it becomes impressive

A second general point is that leaves are nearly always commoner than reproductive organs, except in floras sorted by floating great distances in water, and none of the present floras is of that type It follows that where several unassigned specimens of a reproductive organ are found, its foliage is most probably present in some abundance

Leptostrobus laxiflora and *L crassipes* are both frequent in Heer's flora and they are associated with two species of *Czekanowskia* in two districts, namely, Ust-Balei and Kajamundung The association is fairly close (they sometimes occur on the same blocks), but Heer's text does not show how general and perfect the association may be

Kryshtofovich (1933) figured a specimen of *Leptostrobus laxiflora* and one of *Czekanowskia* apparently from Heer's original locality This confirms the association but does not add to the evidence

I prefer not to rely at all on the various Russian Jurassic fossils described by Schmalhausen (1879) as *C rigida* These include leaf fragments which could be of that or other nature, and fructifications which could be *Leptostrobus* capsules (though others look different)

In the basal Liassic rocks of east Greenland *L longus* occurs as a rare fossil in three localities These are Cape Stewart *Todites* Bed, Storgaad R Plant Bed and Vandekløft *Czekanowskia* Bed The three localities have rather different plant associations, but in all three *C hartzi* is abundant *C hartzi* is, on the other hand, a common fossil in Greenland and is known from fifteen localities

A specimen of *Leptostrobus*, cf *laxiflora* or cf *longus*, has been recorded from Japan by Oishi & Takahasi (1936) and Oishi (1940), from the Liasso-Rhaetic rocks of 'Loc 16 Yamanoi' *Czekanowskia* sp is recorded by Oishi (1940) from 'Loc 1 Yamanoi', the two being of the same age but a short distance apart, there is no mention of *Czekanowskia* in 'Loc 16', the flora of which has not been fully listed I cannot therefore base any argument on this record, though it may be hoped that this matter will be investigated

Turutanova-Ketova (1930) figured an isolated capsule determined as *Leptostrobus laxiflora* Heer in a flora including *Czekanowskia* from the Kirghiz (south-west Siberia) Its age is Jurassic, a good deal younger than the Rhaetic The figure gives no detail

While collecting at Cloughton, by far the best of all the Yorkshire localities for *Solenites*, I looked for and was pleased to find *Leptostrobus* associated with it This locality is a classic one and has yielded quite a large flora, but as it happens no other species which closely resembles *L cancer* in cuticle The actual blocks with *L cancer* have the following species in or near the layers where *L cancer* occurs

Solenites vimineus, overwhelmingly abundant
Ptilophyllum pecten with its flowers (*Williamsonia*) and its bracts (*Cycadolepis nitens*)
Nilssonia tenuinervis (a cycad)
Coniopteris hymenophylloides (a fern)

The block of the Gristhorpe type of matrix in the Yorkshire Museum with *Leptostrobus cancer* is not properly localized, but I am sure it came from the Gristhorpe Bed, since it has the character of that bed at its most typical and is a type of shale known from nowhere else The associated species are among the commonest at Gristhorpe, namely

Nilssoniopteris vittata (Brongniart)
Nilssonia compta (Phillips)
Coniopteris hymenophylloides (Brongniart)
Solenites vimineus (Phillips)

Summary of the evidence of association

Leptostrobus is associated with *Czekanowskia* (or *Solenites*) in eight localities as follows *

East Greenland, basal Lias	3 localities
Yorkshire, Lower Oolite	2 localities
Eastern Siberia, Upper Jurassic	2 localities
South-western Siberia, Jurassic	1 locality

On the other hand, while *Leptostrobus* is a rare fossil, *Czekanowskia* is abundant and has been found in many places where *Leptostrobus* is unknown I have compared the floras of these eight localities, and they have no other genus of leaf in common apart from *Czekanowskia* (including *Solenites*)

Agreement in structure

(1) *Basal scale leaves* Heer is the only author who has seen and figured the basal scale leaves of *Leptostrobus* These scales look very like those at the base of the leafy shoots of *Czekanowskia rigida* and *C setacea* On the other hand, they do not resemble the leaves of any other associated plant

(2) *Cuticle* The studies of various authors culminating in the systematic work of Florin has shown that in the gymnosperms, at any rate, there is a considerable degree of uniformity in epidermal structure over many of the exposed parts of a species The stomata in particular tend to conform to a standard type, and it is possible to use them as well as other epidermal features to relate isolated organs of different categories to one another

Only two species of *Leptostrobus*, *L longus* and *L cancer* have been studied microscopically, and their structure is almost exactly the same

The cuticles of the leaves and of the fructifications agree in the general character of their epidermal cells and in the details of their stomata They differ, however, in the dimensions of the cells and in the frequency and arrangement of the stomata

(*a*) *For* Leptostrobus longus *and* Czekanowskia hartzi

The agreement between the cuticles of the leaf and cone axis is close but it is rather less close between the leaf and capsule wall The leaf has an epidermis with rows of elongated cells with straight, conspicuous lateral walls and a smooth, non-papillate surface The axis of the cone shares these characters The leaf has stomata which are monocyclic (encircling cells are rarely present) The thinly cutinized guard cells have a longitudinal aperture and are sunken at the bottom of an elongated rectangular pit The subsidiary cell group is rather irregular but always elongated, it commonly has terminal subsidiary cells and one or two lateral ones on each side The subsidiary cells are nearly as large as ordinary epidermal cells, but their surface is usually a little thicker Their surface has no papilla, but a small rim of cuticle projects from the lateral subsidiary cells over the sides of the stomatal pit

The stomata of the cone axis are exactly as in the above description, and the dimensions of all their parts is the same as in the leaf They differ, however, in frequency and arrangement In the leaf they are often placed in obscure longitudinal files and they are quite frequent (up to 50 per mm ^{2}) On the cone axis they are very sparse and scattered The capsule wall has larger and much broader epidermal cells, which in some specimens give a suggestion of a median papilla The stomata are larger and relatively broader than on the leaf, but are mostly of the same elongated shape, a few are rounded They are more frequent than on the axis, but again they are scattered, not forming definite files

---

* *Leptostrobus cancer* and *Solenites vimineus* have been found together in a third locality in 1951, namely at Cloughton 30 ft above the Iron Scar

So far as is known trichomes are entirely absent from leaf and cone

(*b*) *For* Solenites vimineus *and* Leptostrobus cancer

Some variation was noticed among the many leaves studied, and the agreement is closest between the cone axis and those leaves with more elongated cells Nearly everything said in the description of *Czekanowskia hartzi* applies equally in the description of *Solenites vimineus*, except that the cell walls though straight often show minute jagged thickenings, and the cells are often not much elongated The subsidiary cell group is often just as in *Czekanowskia hartzi*, but it may be relatively broader, and there is a greater tendency for encircling cells to occur Trichomes are nearly absent, but a very few do occur, and these are confined to the angle of the dichotomy These trichomes are simple, more or less conical prolongations of ordinary cells The cone axis shows elongated straight-walled cells with minute jagged thickenings A very few trichomes occur, and these are simple cylindrical or conical prolongations of ordinary cells The stomata are very few but seem just like the more elongated ones on the leaves, other stomata on the axis seem ill-developed The fruit wall again shows broader cells than either its own axis or the leaf The stomata are rather varied Some specimens show stomata with longitudinally orientated guard cells, rectangular pit and an elongated group of subsidiary cells much as on the leaf, but the whole size and especially the width is greater Other capsules have a large proportion of their stomata of varied orientation and surrounded by a rounded group of subsidiary cells Encircling cells are frequently present, and in some capsules constantly present

I believe that the features of agreement and of disagreement between the cuticles of leaf, cone axis and capsule wall are of just the kind to be expected between different organs of one species

Czekanowskia hartzi is the only Greenland leaf associated with *Leptostrobus longus* with a cuticle closely resembling *Leptostrobus* The next nearest would be *Sphenobaiera spectabilis* (which is found with it in all three localities), but its strongly papillose epidermal and subsidiary cells are very different indeed Other Greenland localities of about the same age do, however, provide a few species with some similarity, namely, *Czekanowskia nathorsti* and *Stenopteris dinosaurensis* Neither, however, is associated with it anywhere and neither is as close to it in structure as *Czekanowskia hartzi*

Solenites vimineus is the only leaf associated with the Yorkshire *Leptostrobus cancer* which resembles it at all in structure The blocks bearing *L cancer* provided the flora mentioned above on p 500 Other Yorkshire localities, however, provide a few species which approach *L cancer* to some extent, these are *Czekanowskia microphylla*, an undescribed *Czekanowskia* of the Upper Deltaic, and *Stenopteris nana* Various Ginkgo and undescribed conifer leaves approach it more remotely

The structural agreement between *Czekanowskia* (or *Solenites*) and *Leptostrobus* is thus very marked and shared by no associated species This structural evidence, taken together with the evidence of repeated association summarized on pp 500, 501, affords circumstantial evidence for supposing they all belong to one group of plants Each additional piece of such supporting evidence adds materially to the probability of the hypothesis I was already convinced in 1935 that there were strong reasons for referring *Leptostrobus* to *Czekanowskia* Since then they have been found associated in two additional Yorkshire localities, an additional Siberian one (the Kirghiz), an additional Greenland one, and perhaps in an additional one in Japan The agreement in structure now extends to a second species

6 Classification of *Leptostrobus* and *Czekanowskia*

Czekanowskia, taken without any fructification, but with the very similar leaves *Solenites* and *Hartzia*, would be easy to classify in the Ginkgoales *Leptostrobus*, on the other hand, is like the fruit of no known plant, recent or fossil, and is in my opinion unclassifiable in any existing family

There has been no dispute about the position of *Czekanowskia* for many years, and Florin (1936) discussed its position exhaustively and decided that he regarded it as an extreme member of the series of fossil leaves assigned to the Ginkgoales I myself have expressed such an opinion

Czekanowskia agrees with *Ginkgo* in the dichotomous plan of its leaf, it has the same general type of cuticle, though this type is by no means exclusive of the Ginkgoales The same may be said of the internal anatomy of the leaf The strongest arguments in favour of its Ginkgoalean alliance is that there is a great series of fossil leaves linking it with *Ginkgo*, and there is little in this series to suggest a division, quite the reverse indeed The reader is referred to Florin (1936*a*, *b*) for a full statement of the points of agreement

Differences are

(1) The lamina is divided into filiform segments

(2) The lamina as a whole is wedge-shaped (with no petiole), while in *Ginkgo* it is distinctly petiolate

(3) The leaves are borne on a short caducous shoot of strictly limited growth In *Ginkgo* they are borne on long shoots or on short shoots of unlimited growth In this respect *Czekanowskia* is like *Pinus* while *Ginkgo* is like *Larix* or *Cedrus*

(4) There are differences in the arrangement of the stomata and in the shape of the subsidiary cell group

(5) Though the leaf of *Czekanowskia* has secretory cavities, their contents is not preserved in macerated leaves In fossil leaves closely resembling *Ginkgo* the resin masses are remarkably resistant to maceration.

(6) The leaf base of *Czekanowskia* has but one vascular bundle, while *Ginkgo* has two

The first five differences seem to me to be of the kind which might all occur in a natural phylum and be rightly used for distinguishing the genera The last difference may be more important

Florin, who discovered this difference in leaf trace number, at first rather discounted its importance. He argued that the Ginkgoales primitively had a single bundle which is seen in these fossil genera, but that in the recent and advanced *Ginkgo* the first dichotomy extended backwards to the stem Later, however (Florin 1949, p 103), he revised his view, as a result of the discovery that in *Ginkgo* the two leaf-trace bundles have a separate origin and are not merely the result of early division He therefore emphasized the possible phyletic importance of this difference between certain of the fossils and *Ginkgo*

Other leaves besides *Czekanowskia* were shown to have a single basal bundle; these include *Windwardia crookallii* and *Arctobaiera flettii*, both of which share with it the caducous short shoot and absence of a petiole The fructification of neither is known Another species with a single basal bundle is *Sphenobaiera hormiana*, but here the material is fragmentary and there is nothing to show how the leaves were borne

The position for the leaf alone is thus *Czekanowskia* is either a member of the Ginkgoales or it is a member of another order with leaves almost exactly like those of the Ginkgoales If it belongs to another order, this order is certainly unknown, and there is no other order with claims to include *Czekanowskia*

The nearest genus, outside the 'Ginkgoales', seems to me *Stenopteris* Several species of *Stenopteris* have leaves with linear, forking segments, and the cuticle is very like that of *Czekanowskia* indeed In *Stenopteris nitida* the midrib of the leaf may dichotomize, and in a series of southern hemisphere leaves placed in *Stenopteris* dichotomy is normal, but there is still a difference in the way the leaf branches In its central region *Stenopteris* branches pinnately, very commonly with opposite pinnae, a kind of branching foreign to *Czekanowskia* (One species, *C microphylla*, shows a slight approach to pinnate branching) Another difference is that the leaves in *Stenopteris* are preserved separately, presumably having been borne on shoots of indeterminate growth, while in *Czekanowskia* they are on caducous short shoots Nothing is known of the rest of the plant in the typical northern species of *Stenopteris*, but the southern hemisphere ones appear to have borne reproductive organs of the *Umkomaasia* and *Pteruchus* groups (Thomas 1933)

No one has suggested that *Czekanowskia* is related to *Stenopteris*, and it is not suggested here, but until both are better understood it is a possibility which should not be excluded from thought

The opinion has already been expressed that *Leptostrobus* is unique and unclassifiable Certain recent and fossil plants do, however, show points of approach or agreement, and these will now be reviewed

Several Bennettitales produce two-valved capsules rather like the capsule of *L cancer*, but less like that of the other species However, instead of a row of seeds, it has been repeatedly proved that there is a row of elongated pollen sacs The way the capsules are borne also is very different, and this comparison will not be pursued

The fossil now named *Harrisia marsilioides* (Harris) Lundblad, 1950 (=*Hydropterangium marsilioides* Harris non Halle) has several striking points of resemblance to *Leptostrobus*, but I believe it has fundamental differences

The main 'axis' gives off branches on all sides (as in a cone), but these branch repeatedly and end in robust two-valved capsules looking very like those of *L cancer.* In view of my mistakes in dealing with *L longus* I reinvestigated some of the slides of *Harrisia*, and I found that one of the *Harrisia* capsules (no 1551) which is slightly immature proves beyond dispute that it is a pollen-bearing organ Every one of the pollen sacs is intact, and each contains many hundreds of the characteristic medium-sized winged pollen grains As a pollen-bearing organ it is separated completely from *Leptostrobus*

It is possible to compare one valve of *Leptostrobus* with any of the following.

a single *Caytonia* fruit,
a *Cycas* megasporophyll,
a *Cupressus* cone scale,
a several-seeded cupule of a Lower Carboniferous Pteridosperm,
a two-seeded cupule of one of the Triassic Pteridosperms (*Umkomaasia*)

In each case it would seem to me possible to start with the embryonic initial of the organ in question (imaginary in the fossils) and to suppose it proceeding by a perverted development to give a *Leptostrobus* valve However, when the two-valved capsule is considered, *Cupressus* and *Cycas* are to be left out, and the series of stages leading to the others become more elaborate, particularly if one valve is really over the other None of these comparisons will be followed in detail because I can see no gain from it, but of course new facts might make it worth while

A comparison with a bicarpellary ovary of an angiosperm is possible, but the differences are great, particularly in pollination, which in *Leptostrobus* is Gymnospermous The approach to an Angiosperm capsule in this Gymnosperm genus does, however, remain interesting as an early organ with much of the biological function of a closed ovary

Leptostrobus is remote from the female fructifications of the Ginkgoales In this group we know (1) *Ginkgo biloba*, (2) a few closely similar fossils associated with fossil *Ginkgo* leaves, (3) certain moderately similar but more branched fructifications associated with *Baiera gracilis* (see Black 1929), (4) similar fructifications associated with *Baiera muensteriana* (see Florin 1949, p 95), and finally (5) *Trichopitys heteromorpha* Sap recently described and discussed by Florin (1949) This remarkable plant bears axillary female 'trusses' which seem to be very like the more richly branched type of female organ found in *Gingko biloba* Microscopic details are lacking, but the appearance of the 'seeds' strongly suggests that they are true seeds and not little seed-bearing capsules like those of *Leptostrobus*

My imagination can only bridge the gap between any of these Ginkgoales and *Leptostrobus* by going right back to a Psilophytalean type of organization of telomes and phyllomes This is another way of saying they seem unrelated

Leptostrobus (with *Czekanowskia*) has in fact the same sort of relation to the Ginkgoales as *Taxus* has to the conifers *Taxus* and its immediate allies agree perfectly with the conifers in their vegetative organs, but the organization of the female organs is so different as to make any relationship too obscure to be profitable to follow at the present time

Leptostrobus requires a new major group to accommodate it, but for reasons given below this group is not yet proposed

(1) It seems very likely that a fresh study of really good material, such as that originally described by Heer, would greatly enrich and perhaps materially alter any characterization at present possible In particular, it is desirable to know more about the organization of the seed It is unfortunate also that male organs are lacking

(2) Such a new group must include the leaves *Czekanowskia*, *Solenites* and probably *Hartzia*, but there is at present nothing to indicate a boundary between the new group and the remaining Ginkgoales For instance, the position of *Arctobaiera* and *Sphenobaiera* would be doubtful and this would be a real disadvantage

Further work may bring to light the fruits of such genera and settle this matter The existing classification of 'Ginkgoalean' leaves including *Czekanowskia* proposed by Florin is of considerable practical value, and though the present work indicates that it includes botanically unrelated plants, this does not necessarily lessen its usefulness

When framed, the characters of the new group will include those of the foliage genus *Czekanowskia* and the cone *Leptostrobus*, but I hope they will include wider knowledge than simply the sum of the diagnoses of those two genera

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DESCRIPTION OF PLATES 18 AND 19

PLATE 18

FIGURE 5 Partly cleared valve showing fragments of two seeds, V 28571 (Magn × 10)

FIGURE 6 Part of the specimen shown in figure 5 showing the chalazal ends of the seeds in each of which a black megaspore is surrounded by a border of integument tissue (Magn × 20)

FIGURE 7 Partly cleared valve showing fragments of four seeds, V 28572 (Magn × 10)

FIGURE 8 Part of the specimen in figure 7 showing the chalazal ends of seeds connected by elongated cells with the valve margins (Magn × 20)

FIGURE 9 Fragment of megaspore membrane showing cell-like folds (unusually marked in this fragment) and conspicuous granules, V 28573 (Magn × 100)

FIGURE 10 Nearly intact megaspore membrane of unusually small size dissected out from a macerated capsule, V 28574 (Magn × 40)

FIGURE 11 Capsule as exposed by cleavage showing a little matrix between the two valves (photo under paraffin), V 28561 (Magn × 10)

FIGURE 12 Capsule isolated by HF and cleared by maceration The valves are somewhat displaced, V 28575 (Magn × 10)

FIGURE 13 Fragment of the fibrous inner membrane of a capsule (which also gave the megaspore in figure 10) The curvature of the upper part suggests a seed integument, V 28574 (Magn × 100)

FIGURE 14 Capsule as exposed by rock cleavage, part of the upper valve is broken away and exposes some of the matrix inside The matrix itself is missing above where the inner surface of the lower valve is exposed *Solenites* leaves occur beside the capsule Photo under paraffin, V 28561 (Magn × 10)

FIGURE 15 Capsule as exposed by rock cleavage, the lower part of the upper valve has broken away exposing enclosed rock matrix Photo under paraffin, V 28561 (Magn × 10)

FIGURE 16 Isolated valve freed by balsam transfer, seen by transmitted light Note the vein-like appearance of the ribs (The same specimen is seen under different lighting in figure 2F) Type specimen, V 28568 (Magn × 10)

FIGURES 17, 18 Two capsules exposed by rock cleavage with different parts of the upper valve broken away exposing the matrix filling the interior Photos under paraffin, V 28561 (Magn × 10)

FIGURE 19 Part of the slab which is believed to have provided the originals of Phillips's figure, pl 7, fig 25 Four capsules in various stages of damage are seen, as well as several leaves of *Solenites vimineus* Photo under paraffin (Magn × 2) York Museum

All the figures are untouched photographs taken by Mr L C Willis

PLATE 19

Figures 21, 28 represent the Greenland specimen of *Leptostrobus longus* previously called *Microchairis enigma* Figure 27 represents *Solenites vimineus*, the rest are all *Leptostrobus cancer*

FIGURE 20 Cuticle of valve wall The stomata in figures 3A to C are from this specimen, V 28569 (Magn × 150)

FIGURE 21 *Leptostrobus longus*, a new photograph of the specimen shown in Harris (1935, pl 8, fig 6) Note the five lobes under each of which is a megaspore, under each of which is a small mass of pollen. The 'fibrous membrane' is broken away at the base of the capsule Greenland slide 2881. (Magn × 12.)

FIGURE 22 Wall of isolated valve in the region of a rib showing fibres and rounded hypodermal cells, V 28576 (Magn × 100)

FIGURE 23 Wall of isolated valve (seen also in figure 16) showing some of the thick-walled cells Drawing on a photo, V 28568 (Magn × 100)

FIGURE 24 Small mass of pollen grains dissected out of the capsule shown in figure 26, V 28578 (Magn × 100)

FIGURE 25 Fragment of associated axis showing broken-off appendage, V 28579 (Magn × 10)

FIGURE 26 Unopened capsule containing dark matter which is chiefly seed megaspores The small masses of pollen are labelled *P* Specimen subsequently dissected V 28577 (Magn × 12)

FIGURE 27 *Solenites vimineus* cuticle, thinner side, V 28591 (Magn × 150)

FIGURE 28 Central part of the specimen shown in figure 21 more magnified The lower ends of the three middle megaspores are seen together with their pollen masses and there are many stray pollen grains adhering to the fibrous membrane Four small round cavities are visible in the megaspores (possible archegonial neck openings) and are labelled *A* Greenland Slide 2881 (Magn × 60) The figure in Harris (1935, pl 8, fig 5) represents the left megaspore and also shows an archegonium like cavity

All figures apart from figure 23 are untouched photographs taken by Mr L C Willis

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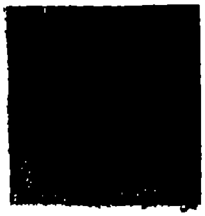
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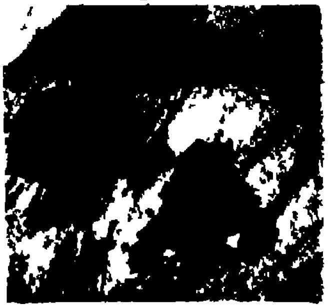
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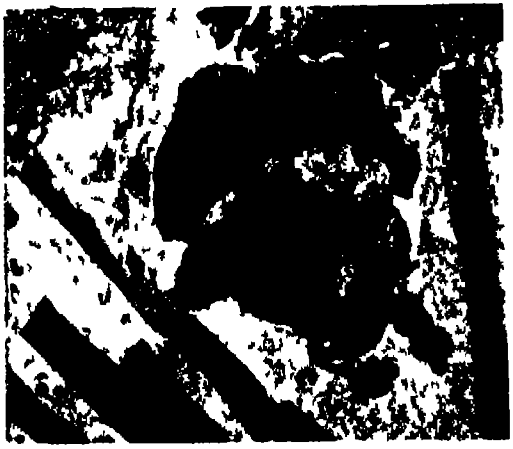
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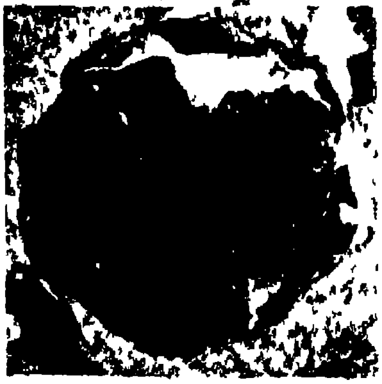
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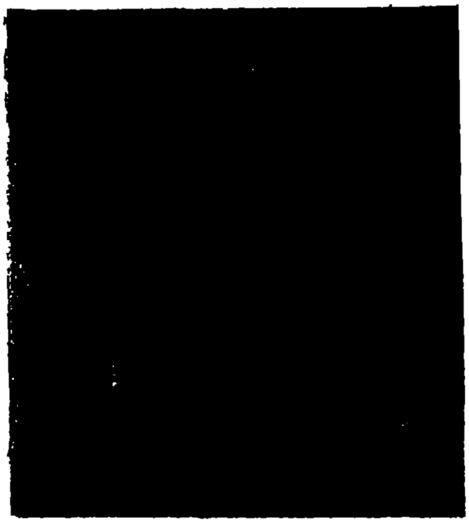
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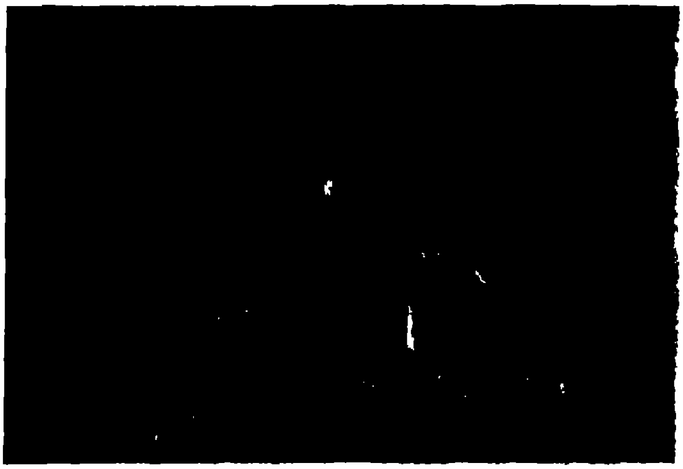
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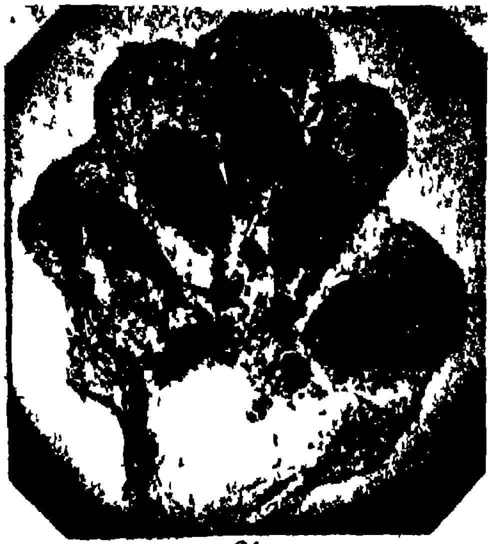
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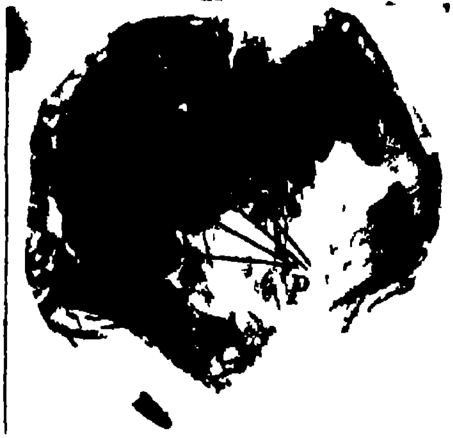

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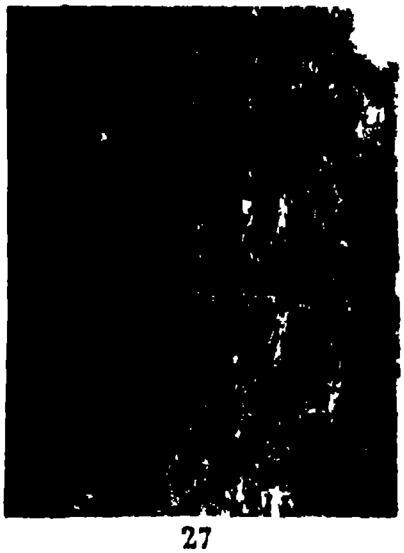
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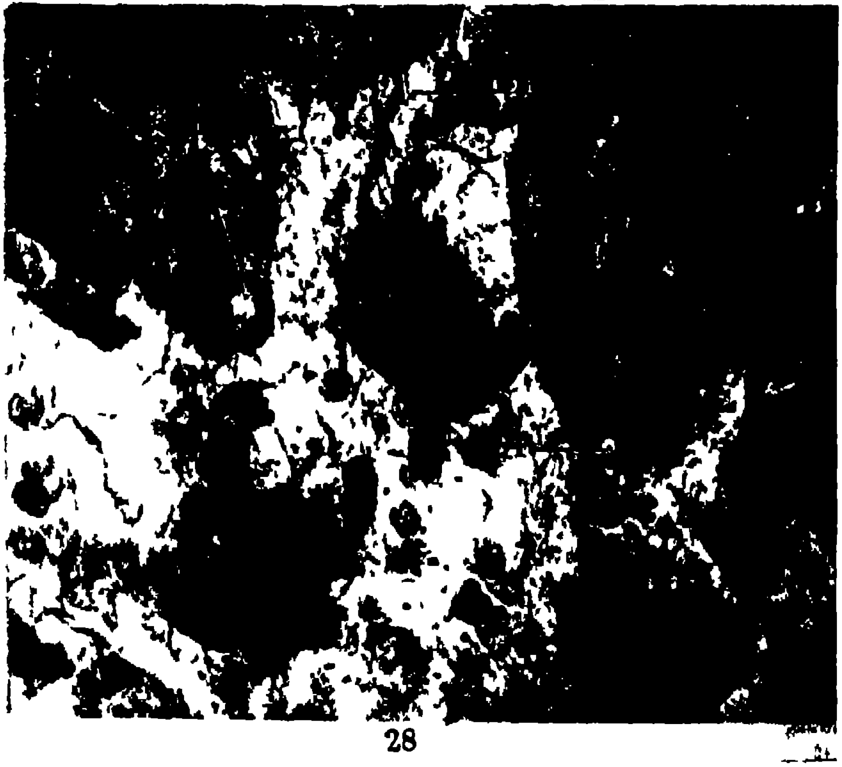
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PHYLLOTAXIS ITS QUANTITATIVE EXPRESSION AND RELATION TO GROWTH IN THE APEX

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(*Communicated by F G Gregory, F R S —Received* 14 *December* 1950)

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Current methods of classifying the phyllotaxis patterns found at stem apices are discussed, and it is concluded that the numerical measures employed do not characterize solely the arrangement or positioning of the primordia, but are partially determined also by primordial shape A method of phyllotaxis assessment is proposed that is free from this ambiguity For a complete description three parameters are necessary, namely, the angle of the cone tangential to the apex in the region under consideration, the divergence angle, and the plastochrone ratio, i e the ratio of the radial distances of two successive primordia from the central axis For assessment of the transverse component of the system the two last parameters are alone required

Of these three characteristics the plastochrone ratio is the most useful, and from it a 'phyllotaxis index' may be calculated that immediately conveys the most essential information relating to the primordial arrangement Since this index is a continuously varying function, phyllotaxis assessment is no longer confined to a few discrete recognized systems, and it becomes possible to compare quantitatively with one another phyllotaxis arrangements of very diverse kinds The relationship between the index and primordial pattern is presented for all important divergence angles, and also for those systems wherein more than one leaf appears at each node

The phyllotaxis index is rigidly related to the ratio of the transverse components of two areas, that of the central apex and that of the newly initiated primordium, a simple extension enables a similar relationship to be determined on the actual apical surface, opening the way for a practical adaptation of the older theoretical concept of 'bulk ratio'

Vol. 235 B 629 (Price 13s.) [Published 25 October 1951

Plastochrone ratio, moreover, is essentially a growth measurement, and in conjunction with the plastochrone period may be used to determine the radial growth rate of the apex, in favourable circumstances it provides all the necessary quantitative information to determine the rate of volume increase

The practical application of these principles is fully considered, the methods being illustrated from measurements made on drawings of apical systems to be found in phyllotaxis literature Tables are appended to facilitate the calculations involved when using the methods described

PART I

1 THE PROBLEM OUTLINED

Assessment of phyllotaxis is a geometrical problem, and particularly so when it is concerned with the simple regular repetitive pattern of the primordia clustered round an apex Like a crystal lattice, all such patterns lend themselves to definition in terms of a few numerical constants, and the attempt has long been made to define in this way the phyllotaxis systems found in growing plants In the classical method of Schimper and Braun only one constant was considered, the so-called *divergence* On an axis having single leaves at the nodes the divergence was defined as that fraction of the circumference which separates two successive leaves in a tangential direction, longitudinal separation along the axis was disregarded In practice, by following the genetic spiral through the consecutive leaf-bases round a more or less elongated stem, two leaves were sought, such that the upper was superposed precisely over the lower, if the genetic spiral made t revolutions between the insertions of these two leaves, separated by n internodes, the divergence was evidently t/n Extensive observations of this kind led to the belief that much the most frequent divergences are those that fall into the series $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$,   , in which either the numerators or the denominators of the fractions, considered alone, are the successive members of the well-known Fibonacci series

An obvious practical objection to the method is the difficulty of determining whether any particular leaf is in fact exactly superposed by some other one, and even assuming that one such exists it is frequently impossible to decide which leaf fulfils this condition In spiral phyllotaxis the few rational divergence angles solely recognized by Schimper and Braun fail completely to describe the true conditions at the plant apex, and presumably this is true also of elongated organs They exist only where orthostichy lines can be found, i e where series of leaves or primordia occur alined along the axis of the stem instead of spiralling more or less steeply round it, and in spiral phyllotaxis no true orthostichies appear Classification by divergence fails therefore because it is based on, and is entirely dependent upon, an incorrect assumption, namely, the presence of orthostichy lines Moreover, it will readily be seen that even if orthostichy lines did exist at apices generally, divergences would supply only very incomplete information about the positions of the primordia there, i e the phyllotaxis, for this depends quite as much on radial as on tangential spacing

For reasons such as these the estimation of divergence angles as a means of characterization was rejected completely by Church (1904) Instead, he pointed out that at the apex itself, so long as growth is uniform and the primordia arise along the genetic spiral at a constant angle, then a whole series of logarithmic spirals may be drawn connecting them Two intersecting sets of these spirals, the *contact parastichies*, are usually conspicuous to the eye, owing to the fact that each primordium touches certain others, because of these contacts the eye tends to select these particular sets and to ignore the other spirals which traverse primordia not in contact with one another Nevertheless, the inconspicuous curves have just as much, or just as little, objective reality as the conspicuous contact parastichies, which are simply a particular pair of sets from among the whole family of logarithmic spirals These curves then are all *parastichies*

The numbers of *contact* parastichies can readily be counted in a transverse section of an apex, and typically give an adjoining pair of numbers from the Fibonacci series, e g five curves running round the apex in one direction may intersect eight others spiralling in the opposite direction Such arrangements Church classified by these numbers of intersecting contact parastichies, the example just given would be designated $(5+8)$, the numbers being connected by a plus sign and bracketed together

Church claimed for this method of expressing phyllotaxis great advantages over that based on the idea of divergence, and, indeed, that it *completely defines* the transverse component of the ordered arrangement at the apex It has been adopted by many subsequent workers, and apparently accepted as an adequate definition of the system, though sometimes the mean divergence angle also is appended Nevertheless, the numbers of contact parastichies define the pattern completely only if Church's phyllotaxis theory holds, and if his particular method of constructing theoretical diagrams really reproduces the divergence angles associated in plants with the various systems According to Church's theory, in the region of initiation one set of contact parastichies always intersects the other *orthogonally*, and each system, e g $(2+3)$, $(3+5)$, $(4+7)$, etc , conforms with a definite divergence angle peculiar to itself Assuming the correctness of these assumptions, the numbers of orthogonal parastichies in both directions do indeed provide sufficient data from which to reconstruct the plan of the apex, i e the 'points of insertion' of the centres of all primordia Moreover, for each such system may be calculated a numerical constant which expresses the size of a primordium relative to that of the meristem on which it arises For this purpose Church used a purely conventional measure, the *bulk ratio*, based on the assumption that each primordium is circular (or '*quasi*-circular') in section and is in contact with each of its four nearest neighbours, bulk-ratio was defined as the sine of half the angle subtended by the approximately circular primordium at the apical centre (cf figure 1*a*, primordia 11, 16, 19, 24) Every phyllotaxis system $(a+b)$ then is associated with a definite and calculable, though entirely conventional, bulk-ratio

There is no evidence, however, that either of Church's postulates holds generally in apices, no support has been forthcoming for the thesis of universal orthogonal intersection, while the presentation by various workers of measurements of divergence angle together with contact parastichy numbers disposes of his second assumption It follows that Church's description, far from defining completely the geometrical pattern at the apex, as he thought, provides little more information than that explicitly stated, viz the numbers of contact parastichies Discarding the principle of orthogonality involves also abandoning the relationship between contact parastichy numbers and the important measure bulk-ratio Nothing can now be posited about radial spacing, though for any given pair of contact parastichy numbers limits may be set to the possible magnitude of the divergence angle, thus a modicum of extra information remains relative to tangential spacing The purpose of Church's mode of approach to the problem fails then almost in its entirety, and for a very similar reason to that which invalidates the approach through divergences: it is grounded in an incorrect theory.

Since the usefulness of the method depends entirely on his theoretical assumptions, and these latter have not been accepted by other botanists, it is perhaps surprising that the method itself should have been adopted. Undoubtedly much of the reason for this is to be

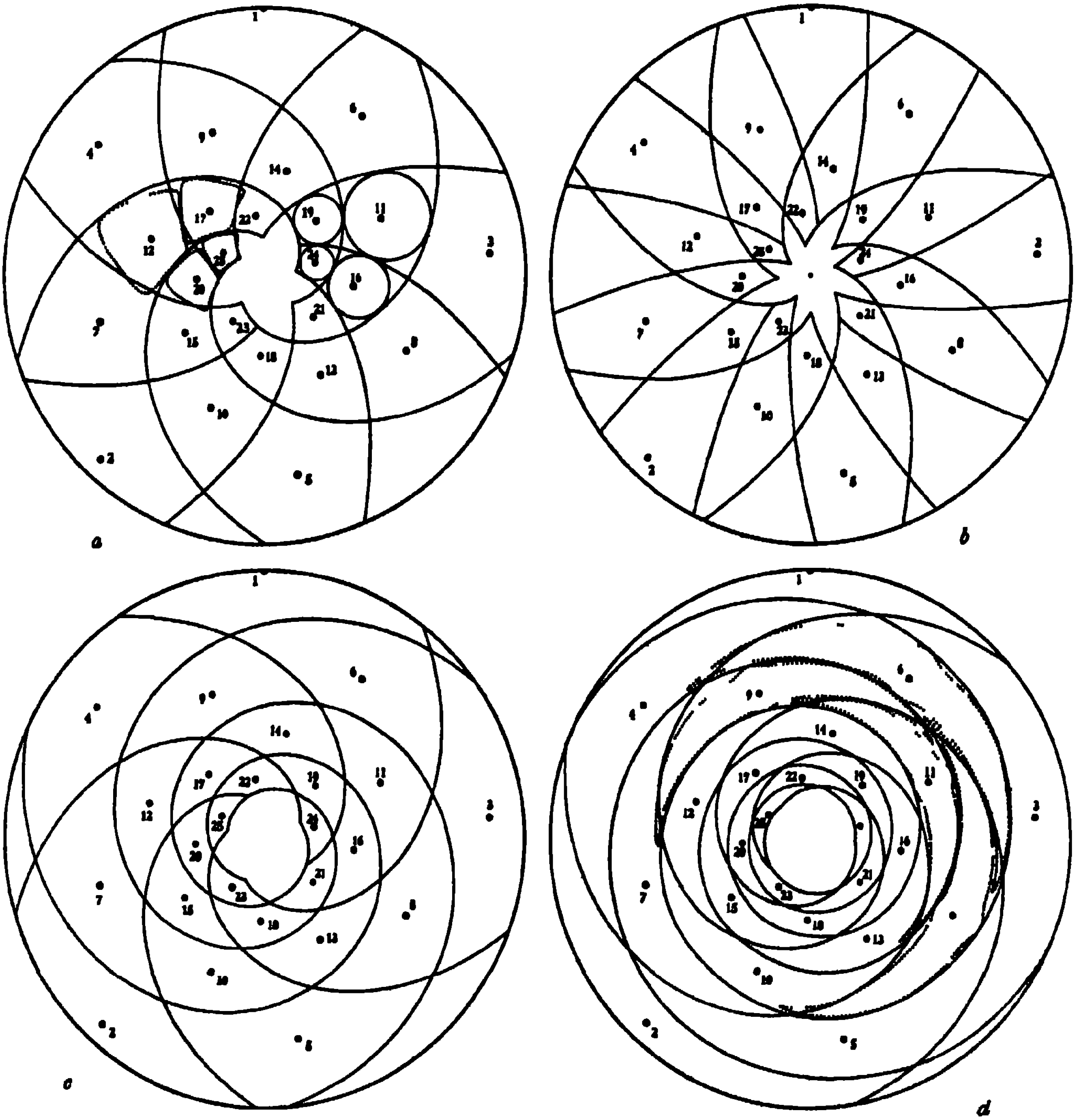

FIGURE 1, *a–d* Ideal representation of the transverse components of four regular Fibonacci phyllotaxis arrangements in all of which the 5-parastichies intersect the 8-parastichies orthogonally. In terms of contact parastichies these arrangements are as follows: *a*, (5 + 8), *b*, (8 + 13); *c*, (3 + 5), and *d*, (2 + 3). Divergence = Fibonacci angle, plastochrone ratio = 1·07296.

found in its simplicity, and the ease with which an apex may be characterized in its terms A further possible reason is the stress laid on primordial contacts, a theme which has been the corner-stone in the theories of several writers since the days of Schwendener

Other writers on the geometry of phyllotaxis (e g Schwendener 1878, Van Iterson 1907, Schoute 1913) have of course recognized the importance to the pattern of bulk-ratio, or of some more or less equivalent measure, but those applied to and utilized in their theoretical constructions are again usually selected in accordance with the particular phyllotaxis theory proposed, they have not been adopted by other workers (and, indeed, could not well be adopted) in the purely practical problem of defining or of estimating the constants of the patterns actually found at plant apices—and yet estimation of this kind is the primary interest in any comparative study of meristems Clearly for these purposes *measures are needed whose validity and usefulness do not depend on the assumptions of some particular phyllotaxis theory*, measures must be sought which are applicable to all, or the great majority, of apices, and which are equally valid regardless of the shapes of the primordia, and regardless also of whether or not those primordia are in contact one with another Because of variability in these latter respects, direct comparisons, as between species, of the relative linear dimensions of primordia and the meristems bearing them are out of the question The measurements adopted then must be of such a nature that they may be determined on actual apices, yet, nevertheless, should convey essential information relative to the apices themselves comparable with that given for purely formal theoretical schemes by bulk-ratio and similar concepts As will be shown, these requirements are met quite simply by applying a geometrical analysis to the system of points marking the positions of the primordial centres (e g vascular strands), using polar co-ordinates in the manner suggested previously by the writer (Richards 1948)

A new theory

Before proceeding with the proposed solution it is perhaps necessary to refer to a recent theory of phyllotaxis due to Plantefol (1948), which has received favourable comment in some quarters (Philipson 1949) Plantefol places the entire emphasis in phyllotaxis on one only of the two sets of contact parastichies considered by Church 'Leaf-generating centres' equal in number to these particular parastichies wind round the apex all in the same direction, and along the course of each arises a succession of leaf primordia, within the apex an organizer maintains uniformity between the activities of these generating centres Hence on the shoot the leaf units come to lie along parallel 'foliar helices', one of which corresponds to each generating centre The phyllotaxis of any shoot is characterized simply by the number of foliar helices

Some defects in the theory have been pointed out by Snow (1948, 1949), and its inadequacy to define phyllotaxis systems on apices should be apparent, for if enumeration of two sets of intersecting parastichies fails to define the system without ambiguity it is evident that one set alone must fail to do so In Church's theory the intersection points of the two sets of curves locate the leaf centres, in Plantefol's no indication is given as to these locations

One of the striking facts of phyllotaxis is that in most spiral systems the mean divergence along the genetic spiral approximates closely to the Fibonacci angle, in other words, the series of leaves obtained by selecting, for instance, every thirteenth along the genetic spiral (where thirteen is a particular number taken from the higher terms of the Fibonacci series) will approach, though not in general precisely realize, the condition described as orthostichous, i.e. the fourteenth leaf will be nearly superposed longitudinally over the first. Plantefol stresses not only that the genetic spiral is an abstraction, a conclusion with which few would now disagree, but, much more debatably, accords it no part in practical discussions of phyllotaxis. Even if his theory be accepted, however, the simple facts of divergence, with the accompanying approximate leaf superpositions, cannot be disregarded altogether. In terms of this theory consideration of 'divergence' along the foliar helices should therefore replace that of divergence along the genetic spiral. Thus, where three foliar helices are recognized, in the large majority of spiral systems (cf. Plantefol 1948, figure 5) the selection of every seventh leaf along each helix will give a line which is nearly orthostichous, i.e. the mean 'divergence' along any one helix is about 52 to 53°, but where there are only two helices (cf. Plantefol 1948, figure 25) it is no longer every seventh, but every fourth or every seventeenth leaf which usually falls on a line nearly parallel with the axis, and there is a mean 'divergence' along each helix of roughly 85°. And so on with other numbers of foliar helices, the introduction of each new curve into an apical system radically alters the 'divergence' along those already in existence, although the divergence proper along the genetic spiral remains substantially unchanged. The concept of divergence cannot then be evaded by the introduction of foliar helices, it is, however, rendered much more abstruse. Before the views advanced can properly be regarded as constituting a theory of *phyllotaxis* it is just as necessary to explain the 'divergences' found along these helices, and their peculiar behaviour when phyllotaxis changes, as it is to account for the Fibonacci angle along the genetic spiral by any other approach. It is clearly insufficient to ascribe these phenomena to an apical 'organizer', with no indication of how the result may be brought about. Unless an explanation is forthcoming there must remain very strong reasons for regarding those parastichies now called 'foliar helices' as less likely even than the genetic spiral itself to indicate the course taken within the apex by certain fundamental entities responsible for leaf production. Valuable as Plantefol's observations may be in the study of the relations between leaf and stem, his views then do not elucidate the problem of leaf arrangement.

2. THE PRIMARY SOLUTION

The kind of geometrical system that needs to be defined, and the inadequacy of the methods of classification in current use, may be illustrated from figure 1. In the four diagrams shown there the numbered points may be taken as representing the centres of primordia. In each figure they are inserted consecutively round the centre of the system at a constant divergence of approximately 137.5° (the Fibonacci angle), and radially at distances from the centre in geometrical progression, the ratio of the progression, working outwards, being 1.07296. Such a ratio between the transverse distance of a primordium from the centre relative to that of the next primordium to be produced has been termed (Richards 1948) a *plastochrone ratio*,* for in a uniform system it is the measure of the radial expansion of the apex at this level during one plastochrone. Since it fixes the radial spacing of the primordia it is likewise a measure equivalent to the bulk-ratio of Church (as will be fully discussed in part II of this paper), but has two great advantages it may be estimated from actual apices, being independent of the shapes of the primordia, and it provides information which is equally applicable whatever theory of phyllotaxis may ultimately be accepted As pointed out in the previous communication, when the factors affecting phyllotaxis are constant the natural logarithm of the plastochrone ratio divided by the plastochrone period gives the *radial relative growth rate* of the apex in the region of initiation, hence for any given divergence angle the arrangement of the primordia, i e the phyllotaxis, may be regarded as a resultant of the relative velocities of two growth processes, rate of expansion of the apex and rate of production of primordia

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* As stated in the earlier communication, Van Iterson (1907) used the reciprocal of the plastochrone ratio in his constructions for plane systems of touching circles. Richards (1948), however, also stated that this particular constant used by Van Iterson was termed the 'relative radius'; this is incorrect. The term was applied to the 'factor *b*' in his constructions, whereas it is his 'factor *a*' which is the reciprocal of the plastochrone ratio.

The actual plastochrone ratio used in all the four diagrams of figure 1, when combined with a divergence angle equal to the Fibonacci angle, results in exactly orthogonal intersection of those parastichies drawn through primordia differing in age by five and eight plastochrones respectively. Logarithmic spirals representing these parastichies have been drawn in figure 1*a*, but between the points instead of through them Thus is produced a theoretical diagram nearly identical with the (5+8) system of Church The area representing the apex is now divided up by spiral lines, crossing always at right angles, into a network, each mesh of which contains one of the numbered points In every mesh it is possible to fit, to a high degree of accuracy, a circle, each such circle touching its four nearest neighbours, as in the construction of Church with its contact parastichies, e g points 11, 16, 19 and 24 in the diagram Not only so, but, as is also shown in the figure, shapes representing the primordia may be drawn which approximate to the outlines of the spiral meshes and yet are also bilaterally symmetrical with respect to the radii of the system through the numbered points The contacts of these areas are essentially the same as those of the circles

But other systems of logarithmic spirals may equally be drawn between the numbered points In figure 1*b* are shown eight curves intersecting thirteen others, figure 1*c* contains three spirals in one direction and five in the other, while figure 1*d* has only two in one direction and three in the other Yet more extreme types could be constructed In every case the meshwork isolates each numbered point from its neighbours, and every mesh contains one of them, also, as shown in figure 1*d*, it is just as possible in each diagram as it is in figure 1*a* to insert shapes representing primordia, bilaterally symmetrical with respect to radii of the system and approximating the outlines both of young leaves and also the spiral meshes An apex similar in transverse section to figure 1*d* would be classified, according to the method generally in use, as (2+3), for these are the contact parastichies, while one similar to figure 1*a* would be termed (5+8), and these two would doubtless be regarded as differing greatly in their phyllotaxis

Nevertheless, phyllotaxis is defined as leaf *arrangement* or *positioning*, and in these four diagrams this is identical, being determined by the numbered points representing the 'centres' of the primordia, which points are fixed absolutely by the two constants divergence angle and plastochrone ratio Again, the positions of the spiral lines have been so adjusted that the areas of the meshes surrounding points similarly numbered (15 for instance) are identical in all diagrams It is readily seen then that these diagrams represent apices

(1) displaying the same divergence angle, (2) whose growth during one plastochrone is the same, and (3) which allot the same proportion of the central meristem to each primordium at its initiation In all essentials relating to manner of growth and to the geometrical arrangement of the primordia the four apices are exactly similar, the only difference between them lies in the *shapes of the primordia*, and phyllotaxis, by definition, is not concerned with these shapes whatever part they may play according to some theories in the production of the pattern, and however much they direct the eye along different spiral lines

Nor must it be supposed that in a system defined as (3 + 5), for example, this definition in itself gives any information about the primordial shape, while it does so in the four diagrams of figure 1, this is solely because these have been constructed with the same plastochrone ratio By varying this ratio, but without altering the divergence angle, 'primordia' of any of the forms shown (as regards their relative extensions in the radial and tangential directions) may readily be obtained displaying any desired contact parastichy numbers taken from the Fibonacci series With a given divergence angle then the contact parastichies depend on two factors, both variable from apex to apex plastochrone ratio and primordium shape, and as a means of defining a phyllotaxis system the contacts are clearly useless without further information Phyllotaxis proper is uniquely defined by divergence angle and plastochrone ratio, if, *in addition*, contact parastichies are stated we have data from which also a very good notion of primordium shape may be inferred

Precisely similar information, both as regards phyllotaxis and primordium shape, would be given by the presentation of divergence angle and number of contact parastichies together with the *angle of intersection* of the latter, for as may be seen from figure 1, the contact parastichies in each of the diagrams intersect isogonally and at a characteristic angle for each The intersection angle is, however, difficult to estimate by direct measurement, nor is the information it provides in so convenient a form as when given via plastochrone ratio, as will be apparent later Very full information of the geometry at the apex would again be available from divergence angle, plastochrone ratio and the angle subtended by a primordium at the centre, but an idea of primordium shape sufficiently good for most purposes is provided by the contact parastichies when considered in relation to divergence and plastochrone ratio, and as the contacts are very readily determined this presentation of the relevant data is recommended as a routine procedure

Before leaving figure 1 it may be pointed out that the diagrams are in essence the equivalent of a simpler straight-line set of constructions, appropriate to mature cylindrical stems, presented by d'Arcy Thompson (1942, figure 452), though the idea goes back much further, at least to Schwendener The present diagrams may be regarded as centric transformations of Thompson's, he did not, however, follow up the implications with regard to phyllotaxis classification and assessment

From the above discussion it is evident that for a divergence equal to the Fibonacci angle a precise relation exists in the transverse plane between plastochrone ratio and the angle of intersection of the consecutive Fibonacci pairs of parastichies A similar relation holds for other divergences and their appropriate parastichies, and may be calculated as follows.

If in a logarithmic spiral the lengths of two radii vectores be v_1 and v_2 and the angle between them be ψ, then

$$\frac{v_2}{v_1} = e^{\psi \cot \alpha},$$

where α is the (constant) angle between the radius and tangent through any point on the curve. This relation applies to all such parastichy lines as those drawn in figure 1, consider one passing through every ath primordium The angle at the centre between two successive primordia along it (ψ_a) may be obtained by deducting the nearest multiple of 2π from a times the divergence angle Expressed in radians this may be taken as ψ in the above equation The corresponding value of v_2/v_1 is the ratio of the distances from the centre of the system of two successive primordia along the same parastichy i e r^a, where r is the plastochrone ratio Substituting these in the equation and taking logarithms

$$a \log_e r = \psi_a \cot \alpha_a, \tag{1}$$

where α_a is the inclination of the tangent of this parastichy to the radius vector, and may now be calculated Similarly for another parastichy passing through every bth primordium

$$b \log_e r = \psi_b \cot \alpha_b, \tag{2}$$

from which α_b may also be calculated If these two parastichies run in opposite directions they interesect at the angle $(\alpha_a + \alpha_b)$, which angle may therefore be determined for any parastichy pair and any desired plastochrone ratio

Should the plastochrone ratio be required at which the parastichy pair a and b intersect orthogonally, equation (1) may be divided by equation (2)

$$\frac{\cot \alpha_a}{\cot \alpha_b} = \frac{a}{b} \times \frac{\psi_b}{\psi_a}$$

Since α_b now equals $(90^\circ - \alpha_a)$, the left-hand side equals $\cot^2 \alpha_a$ Hence

$$\cot \alpha_a = \sqrt{\left(\frac{a}{b} \times \frac{\psi_b}{\psi_a}\right)},$$

and $\cot \alpha_b$ equals its reciprocal Substituting these values in (1) or (2)

$$\log_e r = \sqrt{\left(\frac{\psi_a \psi_b}{ab}\right)} \tag{3}$$

When the divergence equals the Fibonacci angle, a and b may be taken as the nth and $(n+1)$th members of the Fibonacci series, 1, 1, 2, 3, 5, If $n=1$, both a and b are 1, since in the parastichy system 1 1* the two curves travel in opposite directions, ψ_a becomes the Fibonacci angle proper, 222 49224° , i e 3 883222 radians, and ψ_b the same angle, but measured in the opposite direction, i e 137 50776°, ψ_b thus equals $\psi_a \left(\frac{\sqrt{5}-1}{2}\right)$, and it may readily be shown that, whatever the value of n, ψ_b always bears this same relation to ψ_a Hence, for any value of n,

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* A symbolic method of expressing a quite general phyllotaxis system in terms of parastichy numbers must be introduced In Church's nomenclature (adapted from the terminology of the brothers Bravais) the symbol $(a+b)$ implied a system in which the curves referred to were the contact parastichies, which also intersected orthogonally In later usage this symbol refers to the contact relations only, and it is used in that sense throughout this paper (except, of course, when discussing Church's own views) On the other hand, phyllotaxis systems will frequently be defined in terms of parastichy numbers when the particular sets of curves indicated are not, or are not necessarily, contact parastichies In these instances (except for figure 3) the symbol a b will be used It might have been preferable to have adopted Church's symbol without the brackets, but unfortunately these are omitted by some authors even when contact parastichies are under discussion

$$\psi_a = 3{\cdot}883222 \times \left(\frac{\sqrt{5}-1}{2}\right)^{n-1} \quad \text{and} \quad \psi_b = 3{\cdot}883222 \times \left(\frac{\sqrt{5}-1}{2}\right)^{n}$$

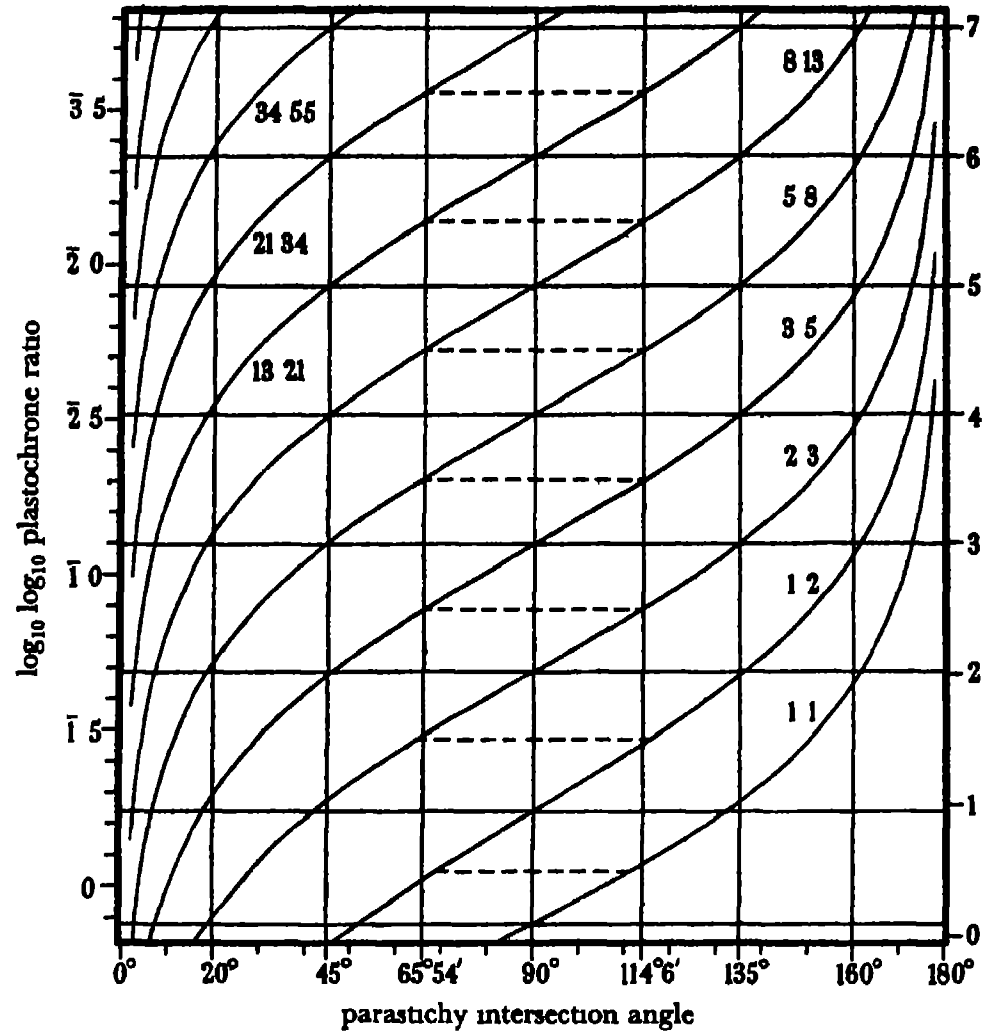

FIGURE 2 The relation, for a divergence equal to the Fibonacci angle, between the double logarithm of plastochrone ratio and the intersection angles of the successive parastichy pairs Phyllotaxis indices are indicated on the right Full horizontal lines are drawn to intersect the various curves at the orthogonal values, and broken lines to meet these curves at the positions at which two consecutive parastichy pairs depart equally from orthogonality

Substituting these values in (3),

$$\log_e r = 3{\cdot}883222 \times \sqrt{\left(\frac{0{\cdot}618034^{2n-1}}{ab}\right)},$$

or, more accurately,

$$\log_{10} r = 1{\cdot}686461920 \times \sqrt{\left(\frac{0{\cdot}618033989^{2n-1}}{ab}\right)} \tag{4}$$

For a divergence equal to the Fibonacci angle the complete relation between plastochrone ratio and intersection angle of each parastichy pair was presented in diagrammatic form in a previous communication (Richards 1948), it is reproduced here with slight modification in figure 2 The parastichy intersection angles are plotted against the double logarithm of the ratio ($\log_{10}\log_{10}r$), since by so doing the curves representing the higher parastichy pairs become virtually parallel and equally spaced, hence the 13 21 curve (or even the 8 13) may represent equally any higher system simply by altering the $\log_{10}\log_{10}$ ratio scale by 0 41798 for each higher step. The full horizontal lines mark those plastochrone ratios at which the various parastichy pairs are orthogonal, while the short broken lines indicate the transitional values, i e. systems in which two consecutive parastichy pairs depart equally from orthogonal intersection

The relation between figures 1 and 2 will be obvious The plastochrone ratio in the former is 1·07296, hence the possible Fibonacci parastichy relations are those defined by the points where the curved lines in figure 2 cross the fifth horizontal line Each of the four parastichy systems shown in figure 1 is thus represented by a single point in figure 2, from which latter diagram their angles of intersection may be read, i e the (5+8) system in figure 1*a* is orthogonal, while the 8 and 13 parastichies in *b* intersect at 45°10′, the parastichies 3 and 5 of *c* at 135° 9′, and finally the parastichies 2 and 3 of *d* intersect at 161° 36′ It will be equally clear from figure 2 that for any phyllotaxis system based upon the Fibonacci angle, plastochrone ratio (and therefore leaf position) is defined by a knowledge simply of the intersection angle of *any* one parastichy pair, as stated previously, by choosing the *contact* parastichies for this, extra information could be given concerning the shape of the primordia For instance, the ratio between the tangential and radial dimensions of the primordia, assuming full contact between them and no intervening spaces, is approximately unity when the contact parastichies are orthogonal and rises continuously with their angle of intersection At 135° the ratio of their dimensions becomes approximately 3 to 1, and at 160° about 8 to 1 However, an improved method of presenting the information supplied by plastochrone ratios is suggested in the following section and for nearly all purposes it is much preferable to take advantage of this, giving the contact parastichies where desired as additional data relating to primordial shape Should more accurate information on this matter be required, other methods of conveying it will naturally be used

3 A SIMPLIFIED DESCRIPTIVE METHOD FOR FIBONACCI SYSTEMS

The primary requisites in defining a uniform phyllotaxis system, as seen at the apex by means of transverse sections, are then the two parameters divergence angle and plastochrone ratio The first presents no difficulty, it has long been associated with phyllotaxis classification, and the fact that the genetic spiral and with it the divergence angle are recognized as abstractions from phyllotaxis theory (and therefore secondary phenomena) in no way detracts from its value as a constant for defining the various systems Experimental evidence has accumulated (Snow & Snow 1931, 1933, Wardlaw 1949, etc) indicating that the characteristic divergence angle must derive from the fact that a new primordium is in the main positioned tangentially by those primordia near to it in preceding cycles or whorls, in such a manner that the angle between the two main determining primordia tends to be divided in a particular and characteristic ratio. This is the primary phenomenon and parameters for purposes of definition might be derived directly from it But in most phyllotaxis systems a single genetic spiral, with divergence angles scattered round a definite mean value, is a consequence of this method of positioning, the mean angle is thus a readily visualized, unequivocal and easily determined parameter providing all the information on tangential spacing needed to construct an idealized representation of the system

The second parameter required, plastochrone ratio, lacks something of the immediate simplicity of divergence angle, and to this shortcoming may possibly be added its unfamiliarity as a botanical concept It is, nevertheless, a most efficient measure and one which is well known as the complement to 'divergence angle' in many geometrical constructions (e g the logarithmic spiral) employing the method of polar co-ordinates Again, phyllotaxis is largely dominated by Fibonacci systems, all classifications of these in the past have been based on Fibonacci numbers, and, indeed, for many purposes some such treatment is both natural and desirable Since all these systems have very similar divergences they differ from one another practically only in their plastochrone ratios But whereas the magnitude of the divergence angle, i e its proximity to 137 5°, immediately conveys the knowledge that a Fibonacci system is under consideration, the accompanying plastochrone ratio, in itself, does not with equal facility indicate to the mind the position of the system under consideration in the Fibonacci scale In fact, of course, that position is fixed by it, and, as may be seen from figure 2 or from the first two columns of table 1, as the plastochrone ratio falls towards unity the parastichy system most nearly orthogonal changes, or rises, from one characterized by low Fibonacci numbers through those with higher and higher pairs of these numbers

TABLE 1

orthogonal system	plastochrone ratio (r)	$\log_{10} \log_{10} r$	phyllotaxis index
1 2	3 79666	−0 2370	0 946
2 3	1 60969	−0 6846	2 017
3 5	1 20451	−1 0925	2 993
5 8	1 07296	−1 5145	4 002
8 13	1 02736	−1 9310	4 999
13 21	1 01035	−2 3495	6 000
21 34	1 003943	−2 7672	7 000
34 55	1 001504	−3 1853	8 000
55 89	1 000574	−3 6033	9 000
89 144	1 000219	−4 0213	10 000

A simple and useful transformation to bridge this mental gap is suggested by the almost uniform spacing of the curves drawn in figure 2 Since the double logarithms of the plastochrone ratios found in any two successive and high orthogonal Fibonacci systems differ by 0 41798, i e $\log_{10}\left(\frac{3+\sqrt{5}}{2}\right)$,* multiplication of the entries in column 3 of table 1 by 2 3925, the reciprocal of 0 41798, must result in a series of numbers almost in arithmetical progression with a common difference of unity If the negative signs are ignored and to each is now added 0 379, the numbers entered in column 4 of table 1 are obtained These derivatives of the plastochrone ratios approximate very closely to the successive integers, and therefore provide immediate information as to position in the Fibonacci scale For this reason they are more useful for descriptive and classificatory purposes than the original plastochrone ratios, yet are easily transformed back to them for growth studies or the construction of theoretical diagrams, etc A number so determined from an actual apex may be called the *phyllotaxis index* of that apex

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* This is easily deduced from formula (4) on p. 518

For practical purposes this index need be calculated to only one place of decimals, indeed, it will not infrequently be found that even this degree of precision is unattainable This being so, all the necessary accuracy in computation is given by the formula

$$\text{phyllotaxis index} = 0\ 38 - 2\ 39 \log_{10} \log_{10} r$$

To the first place of decimals all the orthogonal systems except the first, 1 2, are properly represented by the integers and the error in the remaining one is immaterial, nevertheless, true orthogonality here is found when the value is rather nearer 0 9 than 1 0 If measurements taken on an apex conforming to the Fibonacci angle lead to a phyllotaxis index of 3 0 it may be inferred immediately that the third Fibonacci parastichy system, 3 5, is exactly orthogonal, if the index obtained be 4 5, no parastichy pair intersects orthogonally, but the systems 5 8 and 8 13 are equally removed from orthogonality, again, 5 2 would indicate a phyllotaxis arrangement one-fifth of a unit removed from the 8 13 orthogonal system in the direction of the 13 21 orthogonal, and so on

If desired, these fractional parts may be interpreted directly in terms of the intersection angles of particular parastichy pairs As may be seen from figure 2 the angle between any pair bears a very nearly linear relationship to the double logarithm of the plastochrone ratio, and hence to the phyllotaxis index as well, over the range between the two transitional values 65° 54′ and 114° 6′ This range corresponds to one of a unit in phyllotaxis index, i e from $x-0\ 5$ to $x+0\ 5$, where x is some particular integer Hence over this region one phyllotaxis unit corresponds to rather more than 48° change in the intersection angle of the most nearly orthogonal pair, or each one-tenth unit to about 5° Outside this range the departure from rectilinearity in the relation begins to become evident, but it is useful to remember that a parastichy intersection of 45° represents one phyllotaxis unit below that for orthogonal intersection of the same parastichies, and one of 135° to one unit above that for orthogonality

In the following six sections of this paper the relationships between phyllotaxis indices and parastichy intersection angles in Fibonacci systems will be considered more closely, both as seen in transverse section and on the actual apical surface, also the theoretical phyllotaxis indices appropriate to a variety of non-Fibonacci systems will be derived in order that any obtained from measurements on actual apices may be interpreted without the need for reconstructing the systems If desired, these sections may be omitted on a first reading, the main conclusions reached in them are summarized on pp 536–537 and in the appendix

4 EFFECT OF DEVIATION OF DIVERGENCE ANGLE FROM THE FIBONACCI ANGLE

The above relations hold strictly only for a divergence equal to the Fibonacci angle, 137 50776° With the great majority of apices whose obvious parastichy numbers are a consecutive pair taken from the Fibonacci series, quite regardless of the precise divergence, there is nevertheless only a slight loss in precision if the phyllotaxis index be interpreted as regards parastichy intersection just as it is with the 'ideal' divergence When, as usually happens, the actual divergence approximates to, but is not identical with, the Fibonacci angle, then only a certain number of the lowest of the parastichy systems are geometrically possible, the closer the approximation to the 'ideal' divergence, the greater is the number of possible Fibonacci systems Thus on a centric diagram having a divergence of 135°, all the points representing primordial centres fall on eight radii inclined at 45° to one another, i e the 8-parastichies are radial or orthostichous Similarly with the divergence angle 144°, the 5-parastichies are radial With any divergence between these two limits the 5- and the 8-parastichies form two sets of spiral lines travelling outwards in opposite directions round the centre But outside these limits, when the angle is either less than 135° or greater

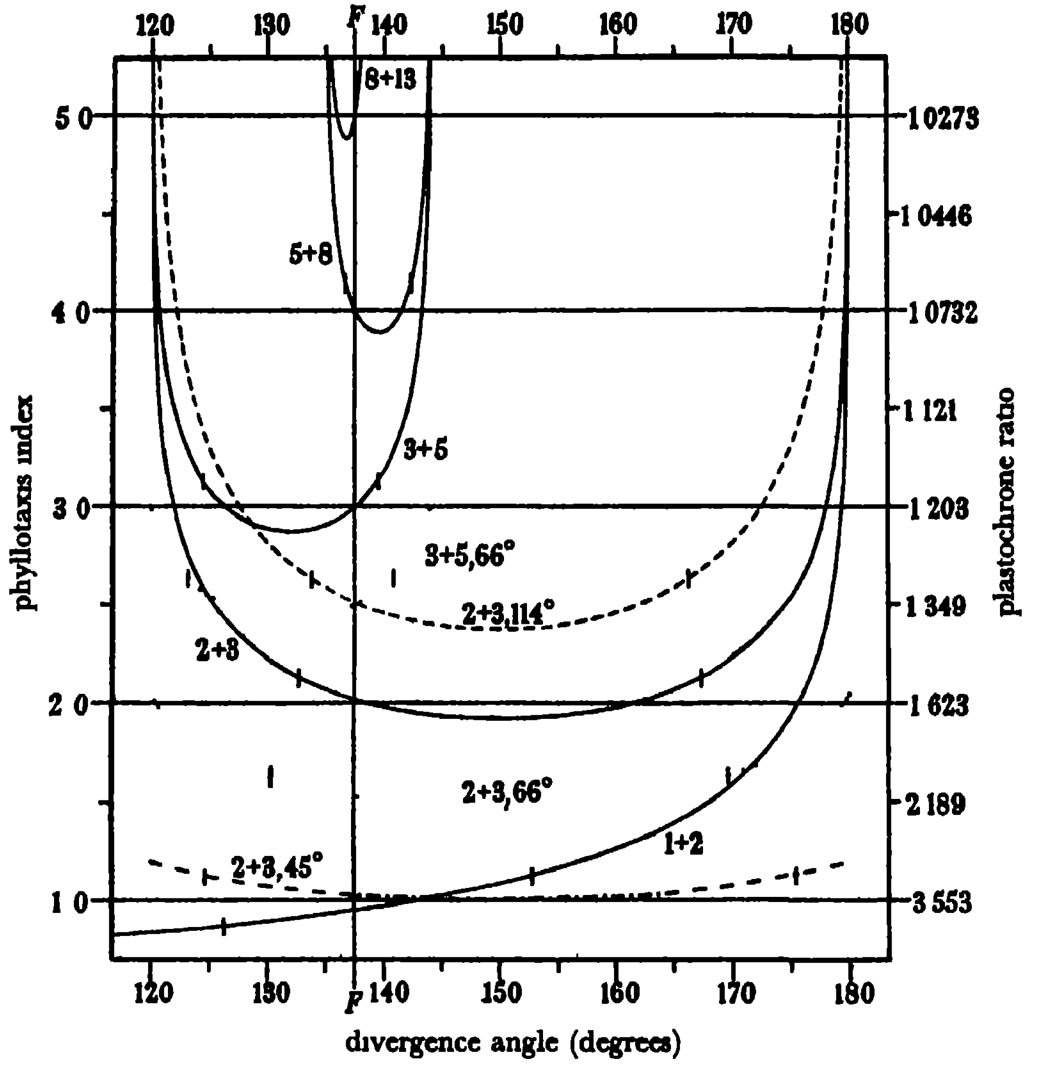

Figure 3 Modification of the relation between phyllotaxis index and parastichy intersection angle in Fibonacci systems due to changes in the divergence angle For further explanation see text The curves should be labelled 2 3, 3 5, etc , instead of 2 + 3, 3 + 5, etc

than 144°, both of the parastichy sets run in the same direction and no system 5 8, as usually understood, exists This, however, does not preclude the existence of lower Fibonacci systems, for the corresponding limiting divergences in the 3 5 system are 120 and 144°, while in the 2 3 any angle greater than 120°, i e between 120 and 180°, is *geometrically* possible The higher the parastichy system, the more restricted becomes the available range in divergence angle within which the two parastichy sets can run in opposite directions, the limits constituting the well-known fractional divergences of the botanical textbooks.

For any given divergence angle and plastochrone ratio (or phyllotaxis index) the intersection angle of any parastichy pair may readily be determined by the method already given (p 517). Figure 3 shows the relationship between phyllotaxis index, over the range 1–5, and divergence angle (between 120 and 180°) for orthogonal intersection of all possible Fibonacci pairs, in addition, curves are presented for 66° intersection of the 2 3 and the 3 5 parastichy pairs, and also for 45 and 114° intersection of the 2 3 The vertical line *F* represents a divergence equal to the Fibonacci angle

Regarding first the full lines representing orthogonal intersections it will be seen that they all cross line *F* very nearly at integral phyllotaxis indices, and that the larger portions of the consecutive curves oscillate to right and left of it Each curve is symmetrical about its own vertical axis, which is situated at the mean divergence angle between its geometrical limits, furthermore, they are all identical in form, so that a single one might be used to represent the whole family, provided the scale of phyllotaxis index be shifted the appropriate amount for each, and that of divergence angle be suitably expanded or contracted

The form of the curves is best seen in that labelled 2+3, they are asymptotic to their divergence limits and are characteristically flat-bottomed Consequently there is a wide range in divergence angle over which the phyllotaxis index deviates by only a small amount from the integral value found near where line *F* is intersected Two points have been marked on each curve, and between them the true phyllotaxis index differs from the nearest integer by an amount not exceeding 0 13 of a unit—an arbitrary amount, but one which is of no great importance in practice Deviations less than this amount are found over approximately 60% of the possible range in divergence angle, but outside the marked limits deviation from the integral value increases rapidly

The only real exception as regards these limits is found in the 1 2 orthogonal curve This is of the same form as the others and is symmetrical round its mean value 90°, but it is situated low, crossing the *F* line appreciably below the phyllotaxis index 1 0, consequently the central region of the curve as well as the outer branches falls ouside the chosen permissible deviation The limiting divergence angles shown for departures of less than 0 13 are about 126 and 153°, but there is another similar range on the other branch of the curve, between about 27 and 54° This need not be considered, for although geometrically possible, phyllotaxis systems with divergence angles below 90° would certainly not be regarded as Fibonacci systems, indeed, they do not exist as 1 2 orthogonal arrangements

Two other curves show the similar relations for intersection angles of 66 and 114° between the 2- and 3-parastichies, in all but the very lowest systems conforming exactly with the Fibonacci divergence these intersection angles are only a few minutes of arc removed from the precise points of transition between two consecutive orthogonal arrangements, as may be seen from figure 2 The curves drawn in figure 3 represent the largest deviations from this condition which it is necessary to consider, yet it is apparent that even these cross the *F* line at phyllotaxis indices very close to 1 5 and 2 5 respectively For a smaller deviation than 0·13 unit from the value 1 5, the 66° curve has a wider latitude of divergence angle than has the 2 3 orthogonal for the same deviation from 2 0 At lower intersection angles still (cf curve for 2 3 at 45°) the latitude increases rapidly, but as the angle of parastichy intersection increases to 114° the permissible divergence range, for this same departure from the phyllotaxis index found at the *F* line, narrows somewhat compared with the range at orthogonality Finally, the 3·5 intersection at 66° is also shown in the diagram, this again is of precisely similar form to the 2 3, 66° line These particular curves are shown as if they ended abruptly at their orthostichous values, they may, however, be continued beyond these divergences, but soon turn upwards towards infinity like the other curves Outside the range shown, of course, the two parastichy sets run round the apex in the same direction, and Fibonacci systems in the usual sense no longer exist The curves representing orthogonal systems run up to infinity (or to a plastochrone ratio of 1 0) at their theoretical limiting divergence angles, here the parastichies in one direction reduce to a set of points and those in the other to a circle

In order to illustrate the change in form of the curves drawn in figure 3 with alteration of the intersection angle of the parastichy pairs, the pair 2 3 has been selected because it is the lowest that need be considered in this connexion in phyllotaxis systems, and because in this case the conditions are the most stringent for the present purpose, namely, to demonstrate that only a comparatively minor error is involved if a phyllotaxis index, derived from an apex conforming with a divergence somewhat different from the 'ideal' angle, is interpreted in regard to the parastichy relations as though (with this same phyllotaxis index) the divergence were in fact exactly equal to the Fibonacci angle In higher systems the proportion of the total range in divergence angle having an error not exceeding 0 13 unit is somewhat greater than in the 2 3 curves shown

TABLE 2

orthogonal system	divergence ranges (degrees) for error < $6\frac{1}{4}$°
1 2	126 3 –152 9
2 3	132 7 –167 3
3 5	124 5 –139 5
5 8	136 7 –142 3
8 13	135 69 –137 77
13 21	137 41 –138 20
21 34	137 244–137 546

It is seen in figure 3 that the ranges of divergence angle, over which a uniform relation between phyllotaxis index and parastichy intersection angle may reasonably be assumed to hold, are very unsymmetrically divided at the Fibonacci angle itself, and that the portion having the greater latitude alternates above and below this angle with the successive parastichy pairs The approximate divergence ranges for the first few orthogonal systems are tabulated in table 2, allowing a maximum error just exceeding 6° (the equivalent of 0 13 phyllotaxis unit) in the intersection angle as immediately deduced from the phyllotaxis index

The range on that side of the Fibonacci angle which has the greater latitude is far wider than is likely to be encountered in any actual Fibonacci phyllotaxis system, but that on the other side may possibly be exceeded in very aberrant apices However, in such a case a limiting orthostichous condition is rapidly approached that will be evident on the plant from the leaves tending to be arranged in 'parallel spires', and in transverse section at the apex by the primordia lying along only slightly curved radial lines Nevertheless, the very large majority of apices exhibiting anything that may be called Fibonacci phyllotaxis display divergence angles falling well within the prescribed limits, and only slight errors will be involved if the parastichy intersections are assumed to be related to phyllotaxis index just as they are when the divergence is exactly the Fibonacci angle

5 PARASTICHY RELATIONS ON THE APICAL SURFACE

The knowledge gained from the phyllotaxis index is confined to the curve system as seen in transverse section, since both plastochrone ratio and phyllotaxis index are defined in terms of the transverse component, and in the absence of further data comparatively little is known of the curve system as it exists on the surface of the apex In some connexions this knowledge is unnecessary, but for others is important In these latter circumstances an adjusted phyllotaxis index may be used to supply the required information, the adjustment being obtained very simply from an angular measurement made on a central longitudinal section of the apex

A typical apical surface is often described as approaching a paraboloidal form, over a small region, such as that where the youngest primordia are situated, it may be regarded to a first approximation as conical The angle at the apex of the cone that most nearly fits the region wherein interest is centred may readily be determined from a longitudinal section, and is sufficient to enable the required adjustment to the phyllotaxis index to be calculated, as the following considerations show

A conical surface has the advantage that it may be unrolled to a plane, if a Fibonacci curve system be drawn on a cone which is then unrolled, the angles of intersection of the curves are unaltered and the plane displays the same parastichy relations as did the conical surface Figure 4 in its entirety represents a 'bijugate' Fibonacci system, and will be considered as such subsequently, but if it be cut along any diameter, say *AB*, then each half may be rolled in such a way that *A* is brought into proximity with *B*, two cones whose apices coincide with the centre of the bijugate system might thus be produced from the diagram In figure 4 the curve system is symmetrical on the two sides of any diameter, the halves are identical in pattern, hence on each of the derived cones the curves will be continuous across the line of junction Each numbered point in the figure formally represents the centre of a primordium, and in interpreting the diagram as two unrolled cones the outer of the two numbers associated with each parastichy intersection point should alone be considered, the inner set of numbers applies when the diagram is regarded as representing a plane bijugate system Using the outer numbers then, in the figure the angle at the centre between points 1 and 2 for instance, or between 3 and 4, has been made equal to one-half the Fibonacci angle, similarly, the angle between point 2 and *A*, and that between *B* and point 3 also sum to the same angle By rolling a semicircle into a cone all angular measurements are doubled, hence each of the derived cones will display a 2 3 parastichy system whose divergence is exactly the Fibonacci angle

In a very similar manner a cone having any desired apical angle and displaying any Fibonacci system may be constructed by drawing this curve system on a sector of a circle of the appropriate size For a cone of apical angle 2θ a sector must be taken whose angular size bears to the whole circle the ratio $\sin\theta$ In figure 4 this ratio is 0 5, or $\sin 30°$, so that the two derived cones would have apical angles of 60°

If then a cone (apical angle 2θ) is to be constructed, on whose surface is drawn, for example, a particular orthogonal Fibonacci system a b, it is now obvious that the divergence angle on the plane drawing must be $\sin\theta$ times the divergence required on the cone All

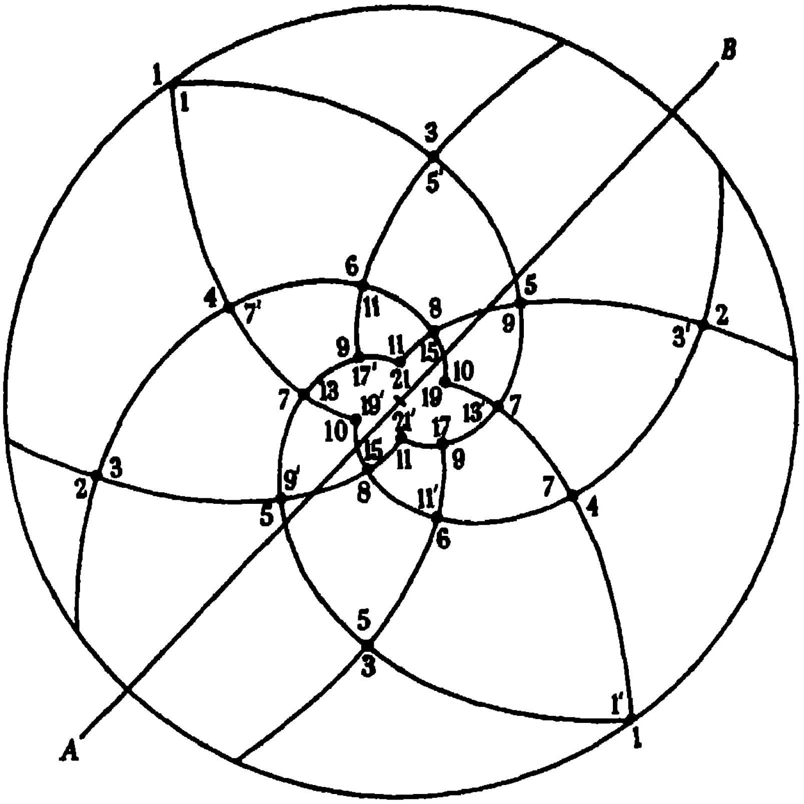

FIGURE 4 Ideal representation of the transverse component of the bijugate orthogonal system 4 6 Any diameter cuts the figure into two identical halves, each of which may be rolled into a 60° cone exhibiting on its surface a 2 3 Fibonacci orthogonal system The inner numbers are appropriate to the plane bijugate figure, the outer to the conical systems

other derivative angles in the system are similarly affected, e g ψ_a, ψ_b, etc (see p 517) become on the unrolled cone $\psi_a \sin\theta$, $\psi_b \sin\theta$, etc Instead of the relation (3) on p 517 we now have

$$\log_e r = \sin\theta \sqrt{\left(\frac{\psi_a \psi_b}{ab}\right)},$$

which gives the plastochrone ratio to be used on the plane drawing

Let X and Y (figure 5) represent two successive points on the cone surface, and X', Y' their projections on the base, then r in the above relation is the ratio of AX to AY By rotating the section $AXX'O$ round AO through the divergence angle, X may be made to fall along AY produced and X' along OY' produced, and evidently $OX'/OY' = AX/AY = r$ But OX'/OY', and therefore r also, is the true plastochrone ratio as measured on transverse sections of the cone, which, together with the divergence angle, defines the system as seen there, or in projection

By hypothesis, however, on the cone surface the Fibonacci system a b is orthogonal For orthogonality in this same system on a full circular plane diagram, as was shown on p. 517,

$$\log_e r' = \sqrt{\left(\frac{\psi_a \psi_b}{ab}\right)}$$

Therefore log r' equals log $r/\sin\theta$, whatever the base of the logarithms, and if r corresponds to a phyllotaxis index of n (where $n = 0{\cdot}38 - 2{\cdot}39 \log_{10} \log_{10} r$), r' will be equivalent to one of $n + 2{\cdot}39 \log_{10} \sin\theta$. Since $\log_{10} \sin\theta$ is always a negative quantity, n is lowered numerically by the adjusting term.

In this expression n is the true phyllotaxis index, as previously defined, and is obtained in practice solely from measurements taken in the usual way from transverse sections, the adjustment, $2{\cdot}39 \log_{10} \sin\theta$, is obtained from the angle 2θ as measured on a longitudinal section. The adjusted index may be termed the *equivalent phyllotaxis index* for the surface, and its sole purpose is to define the curve system existing there, as distinct from its appearance in section. It is the phyllotaxis index which in a plane construction has the same parastichy relations as those displayed on the apical surface, which may therefore be immediately stated.

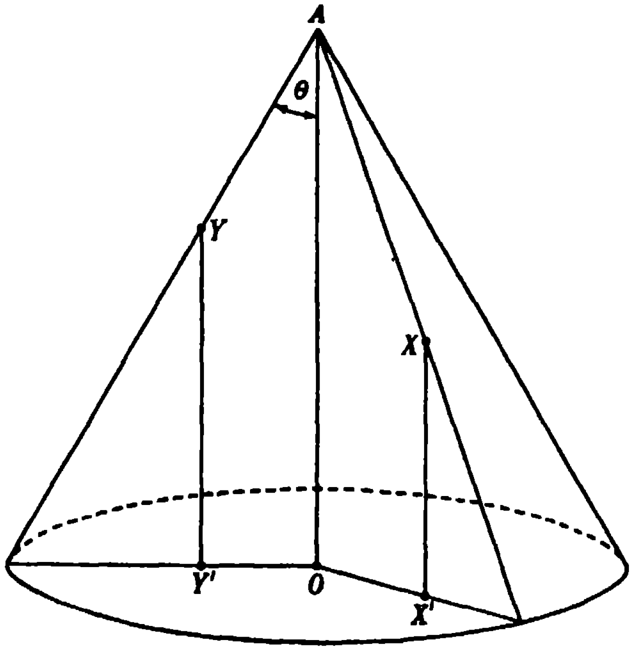

FIGURE 5 Diagram illustrating the relation between the constants of a phyllotaxis system on a conical surface and those of the same system projected on to a transverse plane. See text.

In illustration of the above method, either semicircle in figure 4 may again be considered. If this were rolled into a cone, and the numbered points projected on to the base (cf. figure 5), this plane would correspond to the transverse section of an apex, and the plastochrone ratio as determined on that base would equal that actually occurring in figure 4. This ratio (r) is 1·26875. $\log_{10} r$ equals 0·103376, and $\log_{10} \log_{10} r$ is $\bar{1}{\cdot}0144$, or $-0{\cdot}9856$. Hence n (phyllotaxis index) equals $0{\cdot}38 + (2{\cdot}39 \times 0{\cdot}9856)$, or 2·74, i.e. as seen in section the parastichy system intersecting most nearly orthogonally is the 3 : 5, the actual intersection angle being approximately 77°. Now the apical angle of the cone is 60°, hence the correction factor is $2{\cdot}39 \log_{10} \sin 30$, which equals $-0{\cdot}72$. Adding this to n gives 2·02 for the equivalent phyllotaxis index, which is to be interpreted as if obtained from a plane figure, it indicates then that on the cone surface (or as drawn in figure 4) the 2 : 3 system is exactly orthogonal (cf. table 1).

Values of $\log_{10} \sin\theta$ are frequently presented directly in tables of the trigonometrical functions. Ignoring their negative signs a few are given here in table 3 for cones of apical angle 2θ, together with the corresponding differences between equivalent phyllotaxis index and phyllotaxis index proper, while for practical work the necessary adjustment for any cone may be read from table 3 in the appendix.

TABLE 3

2θ (degrees)	$-\log_{10} \sin\theta$	adjustment in phyllotaxis index
180 (i.e. plane)	0.0	0.0
120	0.0625	0.150
90	0.1505	0.360
60	0.3010	0.720
45	0.4172	0.998
30	0.5870	1.404
15	0.8843	2.116
0 (i.e. cylinder)	∞	∞

It is seen from table 3 that for moderately flat apices the adjustment is not great, amounting even at $2\theta = 90°$ to little more than a third of a phyllotaxis unit, and the apical angle needs to be narrowed to 45° before a difference of a whole unit is found. It follows that over a wide range of apical angle this need be determined with no great precision, for the estimation of phyllotaxis index itself is not profitably attempted closer than to the nearest one-tenth unit. It is apparent also that the fitting of a cone to a part of the apex that is not strictly conical can lead to no serious error, for the change in angle of the 'cone' over the region considered will only be small and the effect on the adjustment trifling. But with apices that taper gradually the possibility of serious error increases, and in the limiting case of a cylinder the method breaks down altogether, since there is here no growth in the transverse direction, plastochrone ratio sinks to its limit at 1.0, and phyllotaxis index rises indefinitely, as also does the adjustment for equivalent phyllotaxis index. This is perhaps unfortunate, since an important group of plants, the Gramineae, is largely characterized by just such apices; these systems can be investigated by the present method only in the region where the axis is expanding laterally, some distance below the zone of primordial initiation.

In more normal apices, however, the investigation could if desired be extended over the whole expanding portion from the apex itself where the primordia arise to the region where transverse growth of the axis ceases. As zones further and further removed from the apex are examined the plastochrone ratio is likely to fall; at the same time the angle of the cone appropriate to the successive zones will narrow, and the resultant estimates of equivalent phyllotaxis index will show whether and how the parastichy relations on the axis surface are changing.

Finally, it should be emphasized that although this discussion of the parastichy relations on the actual surface has been confined to Fibonacci phyllotaxis, the method is equally applicable without modification to all those other phyllotaxis systems whose transverse components are alone considered in the following pages.

6. BIJUGATE AND MULTIJUGATE SYSTEMS

The relation between phyllotaxis index and parastichy intersection angles examined in the preceding sections applies to the large majority of spiral apices Nevertheless, not infrequently apices are found which display truly spiral arrangements but have divergences differing widely from the Fibonacci angle and associated with numbers of conspicuous parastichies not taken from the Fibonacci series In all these the phyllotaxis index supplies information as to the parastichy relations only a little less readily than in the more usual systems

In the first place, apices may be considered whose parastichy numbers are double those found in Fibonacci patterns Figure 4 gives a formal representation of the 4 6 orthogonal system, a duplicated version of the 2 3 orthogonal Fibonacci arrangement Systems of this nature are known as *bijugate*, or are described as being composed of twisted whorls of two members, for at every node two opposite leaves are produced, but those at any one node, instead of alternating exactly with the previous pair, arise at a constant angle to them differing from 90° No single genetic spiral can be put through all the leaves, but two such, situated 180° apart, may conventionally be inserted The numbering in figure 4 illustrates this (inner of the two numbers associated with each point), the points representing the oldest leaves are labelled 1 and 1′ respectively, the next pair 3 and 3′, etc One 'genetic spiral' passes through points 1, 3, 5, 7, , and the other through 1′, 3′, 5′, 7′, These systems tend towards an ideal divergence angle along each 'genetic spiral' of 68 75388° , one-half the Fibonacci angle, and in figure 4 the divergence is of this magnitude From the point of view of phyllotaxis definition, the presence of two 'genetic spirals' needs to be indicated with the other defining constants, for this purpose the divergence in figure 4 might be given as 2 × 68 75°, where the 2 refers to the bijugate condition, and the product indicates the closeness of approach to the primary ideal angle

The assessment of the phyllotaxis index appropriate to the plane curve system figured may be inferred from what has previously been said of the diagram The curve pattern is identical with that of the orthogonal 2 3 Fibonacci arrangement on a 60° cone, the sole difference being that there is twice as much of it, two primordia being initiated in each 'plastochrone' As with the conical construction, a 'plastochrone' ratio may be estimated from the ratio of the distances from the centre of the successive points of foliar insertion, i e the distance of point 1 to that of point 3, or of 1′ to that of 3′, etc Since every 'plastochrone' is double, ratios measured in this way may be supposed to alternate with ratios of exactly 1 0 When comparison is to be made with the plastochrone ratio of unijugate systems therefore, the ratio as measured needs modifying, one part of the appropriate correction evidently being to take its square root, for by so doing the growth made during each double plastochrone is divided into two equal steps, each formally corresponding to the production of one primordium Hence $\log r$ (observed) needs dividing by two, and $\log_{10}\log_{10} r$ (observed) to be reduced by $\log_{10} 2$.

This correction needs to be applied to the value of $\log_{10}\log_{10} r$ appropriate to the semi-circle in figure 4 representing the unrolled 60° cone. This latter has been shown to be derivable from that for the plane orthogonal Fibonacci 2 3 system by adding $\log_{10} \sin 30° = -\log_{10} 2$ (cf p. 527). Hence, starting from the $\log_{10}\log_{10} r$ value for the plane 2 3 system, the total correction to apply in order to obtain a corresponding value for the plane 4:6 system is a reduction of $2\log_{10}2$, or $\log_{10}4$, i e the fourth root of r in any plane Fibonacci system supplies the r value appropriate to the corresponding bijugate system,* for the above argument would hold precisely whatever bijugate system were taken for illustration Since $\log_{10}\log_{10}r$ is negative, deducting from it $\log_{10}4$ increases the numerical value, and phyllotaxis index will be increased by 2 3925 $\log_{10}4$, or 1 440 units, twice the correction appropriate to a 60° cone In any plane system then, a doubling of the parastichy numbers in both directions, without altering their intersection angle, leads to an increase in phyllotaxis index of 1 44 units

Since the plane 2 3 orthogonal system has a phyllotaxis index of 2 02, that of the plane 4 6 orthogonal will be 3 46, similarly, the plane 1 2 orthogonal is indicated by 0 95, and the corresponding 2 4 by 2 39 Higher Fibonacci bijugate systems are orthogonal when the fractional part of the phyllotaxis index is 0 44, e g 6 10 system = 4 43, 10 16 = 5 44, 16 26 = 6 44, etc The point of exact transition between one orthogonal system and the next is marked by a phyllotaxis index terminating in 94, and so on The parastichy relations then may be stated directly from these numbers just as in the Fibonacci systems, but the values at orthogonality are no longer the integers

The correction factor of 1 44 units has been used in deriving the orthogonal values theoretically from those of Fibonacci systems, but it should be made quite clear that in calculating the phyllotaxis index of a bijugate apex from measurements taken on transverse sections, the correction factor to add is only one-half this, i e 0 72 of a unit, which allows for the fact that two leaves appear during each 'plastochrone', or the correction may be applied earlier in the calculation by dividing $\log_{10}r$ (observed) by 2—this will automatically be done in the calculation of r if the primordia present are numbered in the manner shown in figure 4

A plane trijugate system, whose parastichy numbers are Fibonacci terms multiplied by three, may be treated in a similar manner to the bijugate, it may be divided by any three equally inclined radii into sectors, each of which may be rolled into a cone that then displays a Fibonacci system and whose apical angle is twice $\sin^{-1}\frac{1}{3}$ This gives $\log_{10}3$ for the difference between the $\log_{10}\log_{10}r$ (observed) of one-third of the plane trijugate system and that of its full circular Fibonacci counterpart But in the trijugate system r (observed) refers to a triple plastochrone, and the appropriate correction for this is to take its cube root, so, as before, $\log_{10}\log_{10}r$ (observed), a negative number, needs to be reduced by a further $\log_{10}3$ before converting into the corresponding phyllotaxis index Hence the difference in phyllotaxis index between a plane Fibonacci construction and one with three times the number of parastichies is $2·3925 \log_{10} 9$, i.e. 2·283 units, and indices ending in ·28 imply orthogonal parastichy intersection in plane Fibonacci trijugate systems generally.

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* That this is the appropriate correction to apply may perhaps be seen more readily by regarding the bijugate arrangement in figure 4 as composed of two superimposed Fibonacci 2 3 *curve* systems, these two might be dissected apart by selection of alternate parastichy curves in both directions Such a superposition of similar curve systems introduces new points of parastichy intersection, for each set of curves in either original system now intersects not only the complementary set of its own, but also that of the other system Since there are two Fibonacci *curve* systems in figure 4, each with its appropriate set of intersection points, the total *points* in the diagram constitute those of *four* similar interlaced Fibonacci 2 3 systems, i e points 1, 5, 9, 13, , points 3, 7, 11, 15, , points 1′, 5′, 9′, 13′, and points 3′, 7′, 11′, 15′, There are now two genetic spirals, and since the divergence along each is reduced to one-half the Fibonacci angle, each of these spirals maps out two Fibonacci systems in terms of primordia It appears then that in some ways *bijugy* might better have been termed *quadrijugy*, and x-jugy generally, x^2-jugy

It will now be apparent that the phyllotaxis index of any plane x-jugate system is $2·3925 \log_{10} x^2$, or $4·785 \log_{10} x$, units greater than that of the corresponding plane isogonal Fibonacci system, and also, that the appropriate correction to apply, in calculating the phyllotaxis index of any such apex from measurements taken on transverse sections, is either a final addition of one-half this value, $2·39 \log_{10} x$, or else a division of $\log_{10} r$ (observed) by x.

7 Other spiral systems

Sometimes primordia are produced singly in other spiral patterns than Fibonacci arrangements. In these cases the divergence angle most frequently approximates to $\frac{1}{4}\pi(5-\sqrt{5})$, i.e. 99·50155°, and the parastichy numbers are two successive terms of the 'first accessory' series 3, 4, 7, 11, 18, …, a series built up from the first pair of terms in the same way as is the Fibonacci series. In a system of this kind the intersection angle of any pair of parastichies associated with a particular plastochrone ratio, or phyllotaxis index, may be determined in precisely the same manner as was done for the Fibonacci patterns. It may readily be shown that for orthogonal intersection in the system a b

$$\log_{10} r = 0·754208699 \times \sqrt{\left(\frac{0·6180339889^{2n-1}}{ab}\right)},$$

where a and b are the nth and $(n+1)$th terms in the series beginning 1, 3, 4, 7, 11, … The theoretical orthogonal values for all the systems likely to be found are given in table 4.

Table 4

orthogonal system	plastochrone ratio (r)	$\log_{10} \log_{10} r$	phyllotaxis index
3 4	1·2758	−0·9756	2·713
4 7	1·10357	−1·3686	3·653
7 11	1·03741	−1·7972	4·679
11 18	1·014256	−2·2113	5·670
18 29	1·005403	−2·6308	6·673
29 47	1·002063	−3·0482	7·672
47 76	1·000787	−3·4664	8·672
76 123	1·000301	−3·8843	9·672

Just as in Fibonacci and multijugate arrangements, the difference in $\log_{10} \log_{10} r$ between two consecutive systems rapidly approaches the constant value 0·4180. Hence their phyllotaxis indices again differ by one unit. The values at orthogonal intersection approximate to numbers whose fractional part is ·672, and in every case, to the nearest one-tenth unit, this fraction is ·7. Otherwise indices actually found are to be interpreted exactly as in the Fibonacci systems. Small departures of the divergence angle from its 'ideal' value have similar effects on the relation between phyllotaxis index and parastichy intersection angle to those already described for Fibonacci arrangements.

Occasionally the divergence assumes yet other irrational angles, each of which has its own characteristic set of parastichy numbers. One of these may very briefly be referred to, i.e. $\frac{1}{11}\pi(7-\sqrt{5})$. This angle, 77·95525°, leads to parastichy numbers from the Fibonacci-like 'second accessory' series, 4, 5, 9, 14, 23, … The indices at the successive orthogonal intersections again differ by one phyllotaxis unit, those of the higher systems having values whose fractional part is ·179. The two systems deviating most from this rule are the lowest, 4·5 with an index of 3·232 and 5·9 with one of 4·153. Every system therefore has a phyllotaxis index that, to the nearest one-tenth unit, is 0·2 greater than an integer, and indeed from 14·23 upwards, one that to the nearest one-hundredth unit is 0·18 greater than an integer. Similarly with other 'ideal' angles and their accessory series, data for two of which ($\frac{1}{19}\pi[9-\sqrt{5}]$ and $\frac{1}{11}\pi[7+\sqrt{5}]$) are included in the appendix.

In exceptional instances bijugate and even multijugate versions of any of these arrangements may be found. Evidently their theoretical phyllotaxis indices may be obtained by adding the appropriate constants to the values representing the corresponding unijugate systems, just as for the multiple Fibonacci arrangements already considered. An x-jugate system is always 4·785 $\log_{10}x$ units higher than its unijugate counterpart.

8. THE ALTERNATING SYSTEMS

All systems considered hitherto are characterized by irrational divergence angles, or at least by divergences approximating to certain 'ideal' irrational angles. In them all, if phyllotaxis rises (or plastochrone ratio falls) the nearly orthogonal parastichy pairs close up, or increase their angles of intersection, as they do so higher parastichy pairs open out until they become orthogonal, further rise resulting in a similar process being repeated, so that higher and higher parastichy systems pass through orthogonality. The parameter proposed here under the name 'phyllotaxis index' is adjusted to the rhythm common to the systems produced by any of these irrational angles, and especially so to the most frequent set of all, those associated with the Fibonacci angle itself.

Several important phyllotaxis arrangements exist (alternate, opposite decussate, alternating whorls) in which any change of plastochrone ratio cannot lead to the replacement of one set of parastichies by another as the most nearly orthogonal pair, and in these arrangements therefore phyllotaxis index loses something of its significance. It nevertheless remains a valuable parameter, for in terms of it these systems may still be quantitatively compared with spiral systems, and, indeed, quantitative differences may be established even between apices which are usually regarded as displaying the same phyllotaxis, e.g. there is no reason to suppose that all opposite decussate apices have the same plastochrone ratio or phyllotaxis index, and a comparative study within this group might well prove of interest. Rising phyllotaxis will not be reflected here in a change in the number of conspicuous parastichies, but it will *alter the angle of intersection* in the 2 2 spiral system. The relation between this angle and phyllotaxis index is not entirely without interest, and will be elucidated in the following paragraphs, especially as its inclusion completes the survey undertaken in earlier sections.

These various systems from which 'rising' phyllotaxis (in the usually accepted sense) is excluded, all derive geometrically from the fact that a new primordium always appears in a position bisecting angles between the primordia of the preceding whorl; even in the alternate arrangement the new member may be regarded as bisecting the 360° angle round the whole apex terminated in either direction by the centre of the preceding primordium. It follows that the leaves produced at any node are orthostichous with those separated from them by two, four, etc., internodes. All these phyllotaxis systems are then essentially similar, the sole difference residing in the numbers of leaves occurring at the nodes, one in the alternate, two in the opposite decussate, x in alternating whorls of x Hence in the opposite decussate arrangement we are dealing simply with a *bijugate* version of the alternate system, and in alternating whorls of x with an x-jugate version of the same system If the relation between parastichy intersection angle and phyllotaxis index is known for alternate phyllotaxis it may be immediately obtained for these other arrangements by adding the appropriate constants Such constants have already been determined in the consideration of multijugate Fibonacci systems, and the same corrections are applicable here That this is so may readily be appreciated from the fact that a plane centric diagram of an opposite decussate arrangement could be bisected along any diameter, and either half rolled into a 60° cone displaying an alternate arrangement having the same parastichy intersection angle; similarly with a plane diagram of any system of alternating whorls

In the alternate system only two parastichies wind round the apex, and these in opposite directions, each passing through every primordium, the system may thus be designated 1 1 Starting from relations (1) and (2) on p 517

$$a \log_e r = \psi_a \cot \alpha_a \quad \text{and} \quad b \log_e r = \psi_b \cot \alpha_b,$$

it is seen that in this system $a = b = 1$, $\psi_a = \psi_b = \pi$ radians, and $\alpha_a = \alpha_b =$ one-half the intersection angle of the two parastichies Therefore

$$\log_e r = \pi \cot \alpha$$

For orthogonal intersection α is 45°, $\cot \alpha = 1$ and $\log_e r = \pi$, or $r = e^{\pi}$, an interesting conjunction of the two great incommensurable quantities of mathematics Hence for orthogonality in the transverse plane the plastochrone ratio equals 23 14 and the corresponding phyllotaxis index is 0 057 So high a plastochrone ratio presumably never occurs at plant apices, in any event it is scarcely to be expected that growth would continue uniform over so large an area of the apex as it presupposes, and thus the fitting of logarithmic spiral parastichy lines can only be of formal interest here

In Fibonacci phyllotaxis, at the point of exact transition between two orthogonal systems, the pair of parastichies representing one of these intersect at about 114° 6′ A similar intersection angle of the parastichies in alternate systems occurs theoretically with a plastochrone ratio of 7 662, or phyllotaxis index of 0 507, i e a number whose fractional part is almost exactly 5, as in the Fibonacci systems whose parastichies intersect at this angle Further, when any pair of parastichies in a Fibonacci system intersect at 135° the next higher pair is orthogonal, and the phyllotaxis index is almost exactly integral, similarly for intersection at 135° in the alternate arrangement $r = 3$ 674 and phyllotaxis index equals 0 972, or to the nearest one-tenth unit 1 0 In fine, the theoretical relation between the parastichy intersection angle and phyllotaxis index in the 1 1 alternate system is almost identical with that drawn in figure 2 for the 1 1 Fibonacci curve, i e when the divergence is the Fibonacci angle instead of 180° It is, however, displaced very slightly downwards, by an amount that is scarcely larger than the error of drawing This displacement, when measured in terms of phyllotaxis index, amounts at orthogonality to only 0 03 of a unit, and even at 179° to little more than double this quantity Hence in the alternate arrangement phyllotaxis index could be interpreted formally in terms of parastichy intersection angle, to a very close approximation, exactly as it may be for any one pair of parastichies in Fibonacci systems.*

Since this is so for the alternate system it holds also for its multijugate counterparts, and in these, in consequence of their lower plastochrone ratios, the interpretation ceases to be merely formal. The only extra knowledge required is that of the phyllotaxis indices at orthogonality in these systems, obtainable by adding the constants already determined to 0.057, the value in the alternate system. Hence for the opposite decussate (bijugate) and other alternating whorled arrangements orthogonality coincides with the following indices:

orthogonal system	1:1	2:2	3:3	4:4	5:5	6:6
phyllotaxis index	0.057	1.497	2.340	2.938	3.402	3.780

With indices 0.5 of a unit higher than these values, intersection occurs at about 114° (each one-tenth unit accounting as before for approximately 5° increase in the angle over this range), and with indices 1.0 unit higher the intersection angles are increased to 135°, etc. Phyllotaxis indices lower than the orthogonal values listed are unlikely to be found, but if found could be interpreted in an analogous manner.

9. RELATION BETWEEN PHYLLOTAXIS INDEX AND TOTAL PARASTICHIES

From the general expression for $\log_{10} r$ in orthogonal Fibonacci systems (equation (4), p. 518), together with the definition of phyllotaxis index as $0.379-2.3925\log_{10}\log_{10} r$, it may be shown that in these systems

$$\text{phyllotaxis index}=\tfrac{1}{2}n+1.19625\log_{10} ab-0.414.$$

In this expression, as n increases by steps of unity ab increases nearly geometrically, hence among the various orthogonal Fibonacci systems a nearly linear relation exists between phyllotaxis index and the logarithm of the product of the numbers of parastichies in the two directions. Similarly, in orthogonal systems with parastichy numbers from the first accessory series, for instance,

$$\text{phyllotaxis index}=\tfrac{1}{2}n+1.19625\log_{10} ab+0.422.$$

An even closer rectilinear relation exists between phyllotaxis index and the logarithm of the *sum* of the parastichies in the two directions. This is illustrated in figure 6 for all the various orthogonal arrangements discussed previously whose phyllotaxis indices do not exceed 5.0, including multijugate forms up to 5-jugy. Thus examples from a very wide range of phyllotaxis types appear in the diagram, and the closeness with which all the points cluster round a mean straight line is most striking.

In general, however, any three points are not exactly collinear, though certain groups are so. These are the points representing the various multijugate derivatives from each parent system, for example, the Fibonacci derivatives 1:2, 2:4, 3:6, 4:8, lie on one straight line, the systems 2:3, 4:6, 6:9, on another, and the alternating systems 1:1, 2:2, 3:3, on a third, and so on. These lines all have the same slope, which may easily be determined. The difference between the phyllotaxis indices of any x-jugate system and its parent system was shown on p. 531 to equal $2{\cdot}3925 \times 2 \log_{10} x$, where 2·3925 is the multiplier used in calculating the indices and is the reciprocal of $\log_{10}\left(\frac{\sqrt{5}+3}{2}\right)$. As this last equals $2 \log_{10}\left(\frac{\sqrt{5}+1}{2}\right)$ the above expression may be written $\frac{\log x}{\log(\sqrt{5}+1)-\log 2}$. Again, the total

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* This result is not surprising, for we are really dealing with a particular application of the curves shown in figure 3. In 1:1 'Fibonacci' systems the permissible variation in the divergence angle, for a given small error in phyllotaxis index, is very great, so that when this angle deviates to 180° the relation between the index and parastichy intersection angle is scarcely altered, even though a very different leaf arrangement is produced.

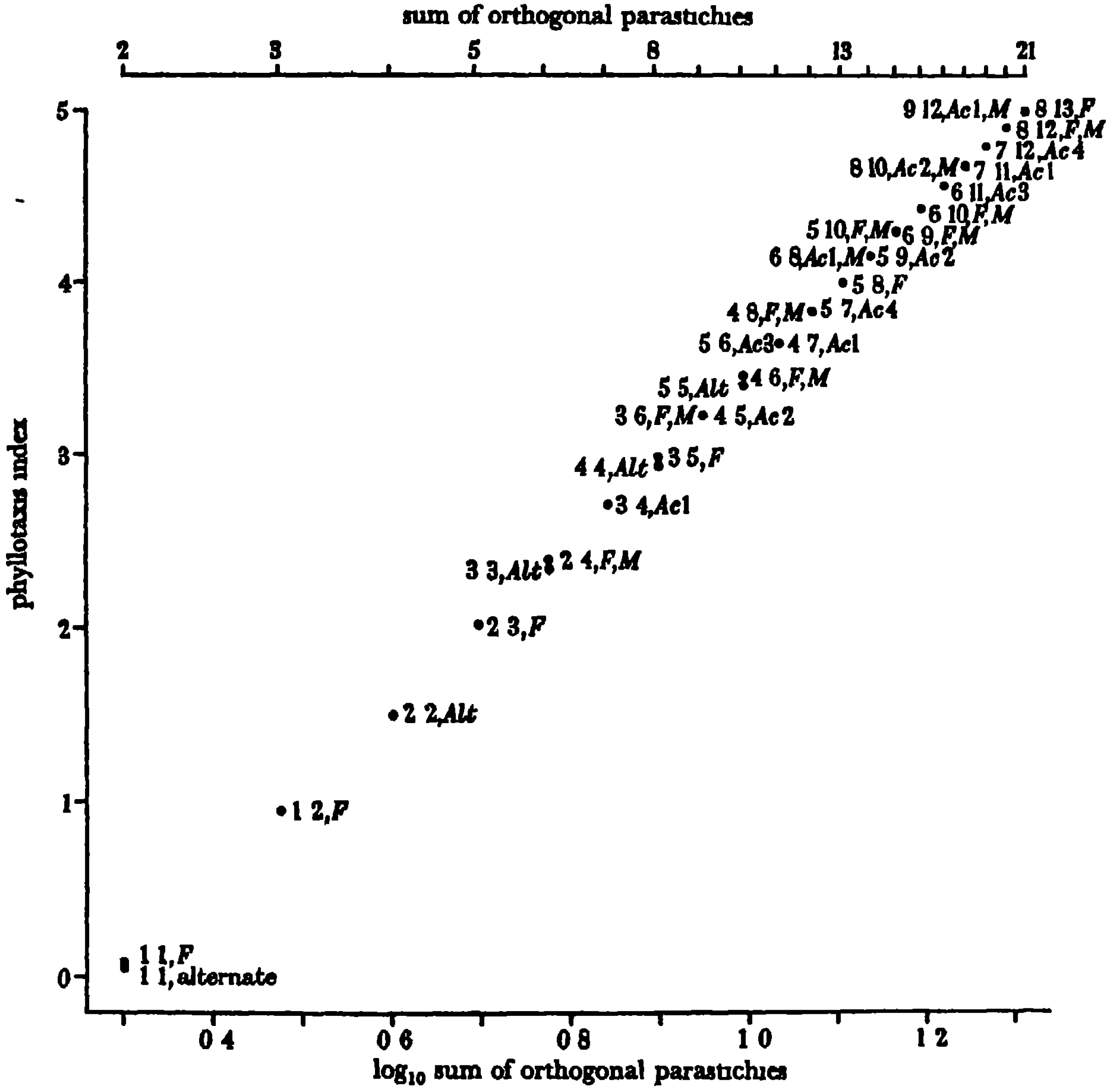

FIGURE 6. Relation between phyllotaxis index and the logarithm of the sum of the numbers of parastichies in a wide variety of orthogonal phyllotaxis systems

F, Fibonacci, ∠ = 137·50776°,
Ac 1, first accessory, ∠ = 99·50155°,
Ac 2, second accessory, ∠ = 77·95525°,
Ac 3, third accessory, ∠ = 64·07936°,
Ac 4, fourth accessory, ∠ = 151·13566°,
Alt, alternating whorls,
M, multijugate variant

parastichy number in the x-jugate system is by definition x times that in the parent system, hence the difference between the logarithms of the total parastichies in the two is $\log x$ The slope of any multijugate line in figure 6 is therefore $\tan^{-1}\frac{1}{\log(\sqrt{5}+1)-\log 2}$, or $\tan^{-1} 4\ 785$

Again, the slope of the line that fits best the points representing the successive orthogonal Fibonacci systems, together with those having parastichy numbers taken from any of the accessory series,* may also be calculated For among both high Fibonacci and accessory systems, if the phyllotaxis index increases by one unit the sum of the parastichies becomes $\frac{\sqrt{5}+1}{2}$ times as great as previously The slope of this line therefore is also

$$\tan^{-1}\frac{1}{\log(\sqrt{5}+1)-\log 2}$$

That is to say, the best line through the starting points (the unijugate spiral systems) of the various parallel lines representing the several sets of multijugate systems is itself parallel to these same lines, and the whole system of points becomes nearly rectilinear The only starting point not included in the above generalization is that of the alternating series, the point representing the alternate series itself, but, as has been shown, the phyllotaxis index for the orthogonal form of this arrangement is very close indeed to that for the orthogonal 1 1 Fibonacci, and so the point comes to lie very near to the line of best fit in figure 6

Thus for all these systems phyllotaxis index appears to be only another way of expressing the total number of parastichies This is of course not generally true In the first place, only orthogonal systems are plotted in the diagram A similar system of points could be inserted for any other constant parastichy intersection angle, yielding another composite line parallel to that shown but displaced in the vertical direction For instance, if the intersection angle of 114° 6′ were chosen, the point representing any system would be raised by approximately one-half a phyllotaxis unit Secondly, each spiral orthogonal system shown has been assumed to be conforming with its appropriate 'ideal' angle, and considerable deviation from this condition might lead to a large vertical displacement But speaking generally, in the spiral systems found in plants phyllotaxis index may be expected to be quite closely related to the logarithm of the sum of the parastichy numbers in the two sets that intersect most nearly orthogonally In the alternating systems this correlation will presumably not be so close, for in them only one set of parastichies is possible and these may intersect at angles very different from a right angle Calling the sum of the most nearly orthogonal parastichies N, and assuming equal deviations on both sides of the line, the regression may be expected to be

$$\text{phyllotaxis index} = 4\ 785 \log_{10} N - 1\ 328$$

10 RECAPITULATION OF RESULTS

The salient points brought out in §§ 4 to 9 may be summarized as follows.

(1) The relation between phyllotaxis index and parastichy intersection angle is not seriously affected by such deviations of the divergence from the Fibonacci angle (or other 'ideal' angle) as are usually found in apices Suggested permissible limits of divergence

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* It is unnecessary to present here a formal proof that the best fitting line for the Fibonacci systems not only has the same slope but is identical with that for each of the sets of accessory systems

angle for the first few Fibonacci parastichy pairs, when each is the most nearly orthogonal pair in any system, are shown in table 2, within these limits phyllotaxis index may be interpreted unhesitatingly as though the divergence were exactly the Fibonacci angle, any error in the parastichy intersection angle deduced being not greater than about 6° Should the limits given be appreciably exceeded orthostichy is approached in one of the two most nearly orthogonal parastichy sets and will become evident in the resulting 'spired' pattern

(2) The parastichy curve system on the apical *surface* may be determined from a knowledge of phyllotaxis index together with the inclination of opposite sides of the apex to one another in the region of primordium initiation—or in any older part of the apex if so desired In table A3 of the appendix are listed correction terms to be subtracted from the phyllotaxis index for various inclination angles of the apex By this operation the 'equivalent phyllotaxis index' of the surface is obtained, this indicates that the parastichy relations on the actual apical surface are identical with those obtaining in a plane construction having a phyllotaxis index equal to it They may therefore be immediately stated

(3) 'Ideal' angles other than the Fibonacci lead to different numbers of prominent parastichies Phyllotaxis index is related to these in a precisely similar way as to the parastichies in Fibonacci systems A change in phyllotaxis index of one unit always indicates a step of exactly one system, so that intersection of the parastichies in the new system remains at the same angle as in the old The Fibonacci systems are unique in that orthogonal conditions correspond with integral phyllotaxis indices, the orthogonal relations for four other divergence angles are given in table A1 of the appendix, thus enabling the index to be interpreted directly in any of these systems

(4) Multijugate systems again are related to phyllotaxis index in just the same way The production of more than one primordium at each node entails a slight complication in the estimation of the index, the necessary adjustment may be made either by adding a constant to the index as directly calculated from measurements on the apex, or by dividing the logarithm of the 'plastochrone ratio' as measured by the number of leaves produced at each node, as explained in the appendix In the same place are also given the data for determining the indices for orthogonality in any multijugate system The opposite decussate is a bijugate development of the alternate system, and alternating whorls of x members provide an x-jugate representation of the same arrangement, these can all be dealt with by the methods described

(5) A close rectilinear relation exists among the parastichy systems belonging to all these various phyllotaxis types between phyllotaxis index and the logarithm of the sum of the numbers of parastichies in the two most nearly orthogonal sets at the apex The relation is illustrated in figure 6

In bringing the theoretical section of this part of the paper to a close, the main advantages of the methods proposed may very briefly be re-stated It is evident that the phyllotaxis index presents all the information relevant to the radial spacing of the primordia at any stem apex Together with divergence angle, the measure of tangential spacing, it completely defines the transverse phyllotaxis system, and defines it in such a way that in any spiral arrangement the parastichy relations involved are immediately apparent It provides a criterion whereby any phyllotaxis system may be directly compared with any other in terms of an essential quantitative characteristic, however unlike the primordial patterns of the two systems may appear. In conjunction with a simple angular measurement taken from a longitudinal section of the apex it enables the curve system as it exists on the actual apical surface to be accurately described, just as readily as is that of the transverse component Furthermore, its counterpart, the plastochrone ratio (into which it is easily transformed), when considered in relation to the plastochrone period, will frequently give valuable information concerning growth rates within the apex Finally, the methods, being based entirely on strict analysis, provide data with which any theory of leaf-positioning must be in harmony The failure of past classificatory systems has been due to their derivation from some particular, and false, phyllotaxis theory, so that the data collected have little more permanent value than the theory itself, indeed, by a regrettable inversion, the facts of phyllotaxis have frequently been falsified in order to conform with the postulates

In § 12 some applications of the methods advocated are illustrated, using published data, but prior to this certain practical points relating to the collection of data are considered in the following paragraphs

11 SOME PRACTICAL CONSIDERATIONS

In the practical determination of plastochrone ratio and phyllotaxis index it is occasionally possible to take the necessary measurements directly from a plan of the apex This is eminently true of many fern apices, for which camera lucida drawings of the region are sufficient In ferns practical difficulties are minimized in a second way, for the apical cell defines the centre of the system, and the distances of the primordia from this centre may be determined with relative ease

Most phanerogamous apices cannot be treated in this way and transverse sections become necessary On a section taken at the level of the younger primordia the positions of the primordial 'centres' are often well defined by the vascular strands, but the determination of the centre of the whole system is a more difficult matter, and the best position can be located only by trial That position must be deemed best from which the distances of the successive primordia fall into the most uniform progression

There is, however, an objection, sometimes serious, to the use of a single transverse section when determining the required distances The leaf primordia are cut at different levels above their insertions on the apex, and unless their bundles all follow a course parallel to the stem axis, measurements of their relative distances from the centre may not reflect sufficiently exactly the transverse growth of the apex in successive plastochrones Serial sections circumvent this difficulty, for then each leaf may be measured at a comparable level close to its insertion The chief objection to this procedure is that the centre of the axis needs determining afresh on each section used, and the several estimates will not exactly correspond Nevertheless, there seems no doubt that it is generally preferable to employ serial sections

It is possible to avoid the determination of the axial centre altogether, for in a system growing uniformly the plastochrone ratio (r) will appear in ratios of other distances on the sections, e g numbering the primordia inversely as their ages, r will be given by the distance of the centre of 3 from that of 2 divided by the distance of 2 from 1 This fact does not generally provide the basis of a good method, for measurements so obtained are affected by inequalities in divergence angle as well as in plastochrone ratio, but on occasion it may be useful; a similar method is always useful in bijugate systems (including the opposite decussate), where the distance across the apex between the members of any leaf pair is very easily determined Again, it is possible that in some plants the ratio of the diameters of consecutive primordia may give a good estimate of r, but usually the primordia do not grow uniformly with the apex, and also change their form in the transverse plane during their first few plastochrones

A simple and easily made measuring device, consisting of a fairly large number of concentric circles with radii in arithmetical progression, is useful in helping to locate the best position for the centre of the system and to speed up the measurements The circles, except for every fifth, which may be heavier, should be thinly drawn in Indian ink on paper and reduced by photography to such a size that they are separated by distances of 1 mm or more, depending on the sizes of the drawings to be measured, care must, however, be taken that the photography does not distort the circles into ellipses The whole is printed rather faintly as a 'ghost' transparency and applied, unbound and gelatine side downwards to avoid parallax, to the drawings to be measured, such an arrangement will neither conceal and confuse the drawings nor unduly dazzle the eye The circles first enable the position of the plate to be adjusted so that the primordia under examination are spaced outwards from their centre as uniformly as possible, and then provide the scale to measure the primordial distances from this point It appears probable that a similar method could be used to measure the sections directly through the microscope, for this purpose the photographic reduction would need to be considerably greater, to a size suitable for an eyepiece graticule, the circles might be printed on film and this mounted between cover-slips

When determining plastochrone ratios oblique sections should be avoided as far as possible Single determinations of r (e g derived from the distances from the centre of primordia 1 and 2, or of 2 and 3) are subject to considerable error, owing largely to the fact that the primordia compared are situated in very different azimuths, one region of an apex may differ slightly from another in its growth and irregularities persist sufficiently long to be reflected in the phyllotaxis pattern, obliquity of the sections would produce a similar effect. Hence measurements in radial directions inclined to one another at only small angles are preferable In Fibonacci phyllotaxis this means that primordia differing in age by 2, or better by 3, 5, 8, etc , plastochrones should be compared, according to the height of the system If now the radial distances of two primordia differing by three plastochrones be measured, the plastochrone ratio is given by the cube root of the ratio of the measurements

A better estimate could be obtained by finding log r as given by each of the pairs of primordia 1 and 4, 2 and 5, 3 and 6, and taking the mean of the three derived estimates before converting to phyllotaxis index Finally, in order to achieve the greatest accuracy a slightly more laborious method may be used, and particularly so if the change in phyllotaxis index or plastochrone ratio is to be followed as the primordia recede farther and farther from the apex. The distances of all the primordia over the required range may then be recorded and their logarithms taken; provided there is no appreciable evidence of the increment in these distances decreasing with increasing plastochrone number, a straight-line regression may be fitted, relating log distance to age in plastochrones The slope of this regression provides the best estimate of log r The arithmetic is simple, an example being worked out later (p 541) Should the increment decrease with distance from the centre a curved regression will enable the best value at any plastochrone age to be determined (see p 560)

In order to obtain knowledge of the curve system on the apical surface the phyllotaxis index obtained as above may be converted into the equivalent phyllotaxis index for that surface The angle of inclination towards one another of opposite sides of the apex in the region under consideration is then required (2θ), and may be obtained easily from a longitudinal radial section This method, however, involves collecting the two sets of required data from different apices, and to this extent is unsatisfactory If the measurements for phyllotaxis index are made on serial transverse sections of known thickness, the latter may also be used for determining the angle of inclination required Thus if d_1 is the radial distance of one primordium at its insertion level and d_2 is that of another, and the higher measurement is made on the nth section above the lower, each section having a thickness of h, then $\tan\theta = \frac{d_1 - d_2}{nh}$ From either 2θ or $\tan\theta$ the appropriate amount to be subtracted from the phyllotaxis index may be read from table A3 in the appendix It is, however, especially important to note that if transverse sections alone are used, oblique cutting must be scrupulously avoided

12 ILLUSTRATIONS OF THE METHOD

A few illustrations follow of the application of the above methods to certain published phyllotaxis data, though it should be borne in mind that these data were not collected for the purpose and so do not provide ideal material

(*a*) *Dryopteris aristata*

As a first example may be taken the apex of the fern *Dryopteris aristata*, which presents a dilemma when classification is attempted by the method in general use, i e the numbers of contact parastichies in the two directions The primordia are in fact very far from being in contact one with another, each being separated from its neighbours by an expanse of bare apical surface It has already been pointed out (Richards 1948) that methods involving the use of plastochrone ratios provide the sole means of classifying and assessing such systems Wardlaw (1949, p 171), however, writes concerning his own text-figures 5 and 6 'it would be more accurate to describe [primordium] I_1 as originating between [primordia] P_3 and P_5, rather than between P_2 and P_3, although the latter description is not incorrect', and again, on p 188 concerning his text-figure 44, 'In a phyllotactic system of this kind some investigators would no doubt regard P_2 and P_3 as the "contact" primordia But direct observation of fern apices indicates that the primordia immediately adjacent to I_1 are P_3 and P_5' Clearly such a position is unsatisfactory, for in dicotyledonous apices there is no guarantee that the contact system of primordia is the same as the system of *nearest* primordia, when distances are measured from their central regions, that this is not always so is readily seen from figures 1*c* and *d* Some other method of assessing phyllotaxis is essential if comparison is to be made between the apices of leptosporangiate ferns and those of flowering plants

In Wardlaw's figure 4, five primordia are represented together with the position of the apical cell Measurements on the drawing give relative distances from the centres of these primordia to the apical cell as shown in column 2 below, and the logarithms of these distances are given in column 3. In order to determine plastochrone ratio and phyllotaxis index the extreme values might be chosen, relating to primordia 1 and 5. The difference of their log distances divided by the difference of their ages in plastochrones gives the mean $\log_{10} r$, i.e. $\frac{1}{4}(0·702-0·589)=0·02825$. Hence the estimate of plastochrone ratio becomes 1·0672, the corresponding phyllotaxis index is 4·08. Table A4 in the appendix may be used for converting the estimated $\log_{10} r$ into phyllotaxis index, giving 4·1.

primordium (P)	relative distance	$\log_{10}$ distance (L)	P^2	$P \times L$
1	3·88	0·589	1	0·589
2	4·11	0·614	4	1·228
3	4·50	0·653	9	1·959
4	5·10	0·708	16	2·832
5	5·03	0·702	25	3·510
total 15		3·266	55	10·118
mean 3			45	9·798
			10	0·320

$$\log_{10} r = \frac{0·320}{10} = 0·0320$$

The $\log_{10}$ distances in column 3 show that although the mean increment is 0·02825, individual increments differ rather widely from this value, indeed, primordium 4 is situated slightly farther from the apical cell than is number 5, which is presumed older. When irregularity is as great as here, it is advisable to fit a regression to the data, as by this means equal weight is given to the evidence provided by each primordium. The arithmetic, worked out above, is particularly simple, for the independent variate, primordium number, consists of the successive integers. The best estimate of $\log_{10} r$ derivable from the data is given by the ratio of the numbers derived in the last two columns, in this instance 0·0320. Hence phyllotaxis index becomes 3·95 and plastochrone ratio 1·0765.

The general level of the index indicated in the above example is confirmed by measurements taken from other apices figured by Wardlaw (1949). Thus by applying the regression method to measurements relating to the last eight primordia shown in his figure 1, an estimate of 3·80 has been obtained, similarly, from the last ten primordia of the apex drawn in his figure 5 an index of 3·87 has been derived.

The statistical error of $\log_{10} r$ in each of these estimates may of course be calculated, and from it the limits of phyllotaxis index within which the 'true' value for the apex may be assumed to lie with a given level of probability. The example worked out above, which was chosen largely because of the aberrant positioning shown by some of the primordia, has an unusually low precision, and for a probability level of 0·05 the fiducial limits of the index are 3·5 and 4·7; for a probability of only 0·2 the range becomes restricted to 3·71–4·27. The other two apices mentioned have considerably lower errors, the index range for 0·05 probability being 3·63–4·00 in Wardlaw's figure 1, and 3·66–4·14 in his figure 5. The results from these apices thus reinforce one another, and it may be assumed with some confidence that the best value lies between 3·8 and 3·9, or only very slightly outside these limits.

Wardlaw's figure 6 presents an 'idealized phyllotactic system' for comparison with the real apex of his figure 5. In this diagram, however, only the divergence angles have been equalized, for the increments in log apical distance between the first ten primordia vary irregularly over the approximate range 0·025 to 0·08. The regression method yields a phyllotaxis index for the diagram of 3·51, and indicates a distinctly lower system than that of the real apex it illustrates, the best value lying outside the probable range given in the previous paragraph for the real apex; indeed, the difference between the two drawings in this respect is appreciable to the eye. A further 'ideal' arrangement of primordia is presented in his figure 40, and from this an index slightly above 3·9 has been obtained, which may perhaps be considered as confirmatory evidence of the general level in these apices.

Phyllotaxis indices of 3·8 to 3·9 then are indicated by the drawings, and it follows that as seen from above the 5 8 system of parastichies in these apices is much more nearly orthogonal than the 3 5, their intersection angle being over 80°. In the same article Wardlaw (1949, figure 2) presents a semi-diagrammatic drawing of a median longitudinal section. The apical cone, on whose lower flanks the primordia are produced, is comparatively broad, having an angle of 98°, so that $2·39 \log_{10} \sin 49°$, or 0·29, gives the amount to be deducted from the phyllotaxis index proper in order to obtain the equivalent phyllotaxis index of the surface towards the base of the apical cone (from table A3 in the appendix the correction may be read as 0·3). The equivalent phyllotaxis index thus becomes 3·5 to 3·6, that is to say, on the surface in the region of initiation the parastichy systems 3 5 and 5 8 are almost equally removed from orthogonality, though probably the higher system is a little nearer orthogonality than the lower. In choosing the system 3 5 rather than 2 3 Wardlaw has not therefore overstepped the evidence provided by the apices, on the contrary, any argument that might exist lies between the claims of 3 5 and 5 8. But the statement that the equivalent phyllotaxis index is 3·5 to 3·6 leaves little room for uncertainty, and the intersection angle of either parastichy pair on an idealized apex may be stated with only a narrow margin of error.

This method of dealing with phyllotaxis carries with it also interesting implications regarding growth rate within the apical cone. Provided the apex remains constant in size, or nearly so, i.e. that the successive primordia are initiated at the same distance from the apical cell (and there is no reason to suppose this is not substantially correct in the present instance), then the natural logarithm of the plastochrone ratio is the transverse linear relative growth rate of the lower part of the apical cone, time being measured in plastochrones. Twice this value gives the corresponding growth rate of the transverse area. Again, the maintenance of a given conical form at an apex implies very strongly that in any frustum the longitudinal growth rate equals the linear transverse rate. For if the longitudinal rate is higher than the transverse the form of the frustum will change and the apex as a whole may be expected to deviate towards the shape usually described as paraboloidal, the flanks becoming convex in the longitudinal direction, while if the longitudinal rate is lower than the transverse the flanks will become concave in this direction. Hence in the apical cone of *Dryopteris* it may legitimately be assumed that the growth rates in all directions are approximately equal, and that the volume relative growth rate per plastochrone is roughly $3 \log_e r$. Since for a phyllotaxis index of 3·8 to 3·9, $\log_e r$ equals 0·082 approximately (appendix, table A4), this indicates the relative rate of radial increase per plastochrone, and the corresponding volume increase is 0·246. As $\log_e 2 = 0·693$, the time taken for a given frustum of the lower part of the apical cone to double its volume is 0·693/0·246, or 2·82 plastochrones approximately Since Wardlaw (1949, p. 171) states that his specimens 'formed new primordia at the rate of about one per week', this implies a period of about 19 to 20 days On the data presented then it appears that the *minimum* period that must be assumed to elapse between two consecutive divisions of the same cell towards the base of the apical cone (i e in the event of there being no growth by cell enlargement) is on the average nearly three weeks, the average cell in the interior of the cone remains quiescent while about three primordia are being produced at the surface

(*b*) *Lupinus albus*

A second illustration may be taken from the experiments of Snow & Snow (1931, 1933) on *Lupinus albus* On p 4 of the first of these papers it is stated that the 'contact parastichies of *L albus* form a 2+3 system The leaves have stipules which extend round the axis, so that the stipules of successive leaves are in contact with each other If the stipular contacts are included, the contact parastichy system becomes 1+2+3 The primordia arise as circular humps, with the stipules forming tapering horizontal projections on either side The whole primordium is thus roughly oval in shape with its longer diameter lying transversely to the axis of the shoot' Even in dicotyledons then, with the leaf members making close contact everywhere, the correct position in the binomial classificatory system may be doubtful Moreover, the drawings of transverse sections presented, and also the diagrams showing the contact relations as seen in surface view, indicate clearly that while the central parts of the primordia are in contact along the 3-parastichies, they are far from being so along the 2-parastichies Hence if the system be described as (2+3), one of the contacts referred to is made by the central parts of the primordia only, while the other involves a stipular contact For this reason it might perhaps seem preferable to regard the system as (1+2), these being the overall stipular contacts, rather than (2+3) However, for purposes of classification and assessment at least, it is advisable to avoid the difficulty altogether and to use a system leading to an unambiguous conclusion This is not to say that information regarding the actual contacts is either valueless or superfluous—indeed, for some purposes it may be important—but that it is information which by itself gives no clear idea of *phyllotaxis* proper, in conjunction with such a measure as phyllotaxis index it provides very full data indeed as to the geometry at the apex

Estimates of phyllotaxis index may be obtained from several of the sectional drawings of apices presented by Snow & Snow, the methods used are similar to those adopted when assessing the *Dryopteris* apices of Wardlaw, but owing to the fact that transverse sections now replace the plan of the apex, for reasons given above (p 538) it is necessary to confine the measurements to a smaller number of the youngest primordia At least this is so when, owing to the fact that only a few isolated sections from any apex are presented, the measurements must be confined to a single section This may well increase the error of determination, although in fact the *Lupinus* apex appears to be more regular than that of *Dryopteris* A number of determinations on single sections have led to phyllotaxis indices ranging from 2·8 to 3 3, and usually a little higher than 3 0

For a few of the apices depicted, however, it is possible to obtain estimates derived from two sections, using two selected primordia each measured at the particular level where it is just breaking completely free from the axis. Such an estimate may be compared with a similar one derived from the same two primordia, but in this case taken from a single section, the upper one of the two previously used The estimate derived from two sections appears to be a little higher than that derived from a single one.

	phyllotaxis indices from four apices			
single section	3 30	3 26	2 99	2 83
two sections	3 39	3 61	3 17	3 04

The mean difference is 0 2 of a unit Accepting this value and applying it as a correction to the more numerous estimates based on single sections, it appears that the phyllotaxis index of a typical *Lupinus* apex as used by Snow & Snow is about 3 2 to 3 3, in plan the 3 5 system of parastichies intersects at 100 to 105°

A few longitudinal sections of *Lupinus* apices are presented by Snow & Snow, and others are given by Pilkington (1929), from them estimates are obtainable of the apical angle of the cone that best fits the region of primordial initiation Unfortunately for the present purpose these apices had usually been mutilated some time before sectioning, a fact that may possibly account for a rather high variability among the estimates derived from them The angles measured are respectively 48, 48, 52, 56, 58, 59, 60, 63 and 78°, with a mean of 58° Hence the equivalent phyllotaxis index of an average apex is about 3 25 − 0 75, or 2 5, and on the apical surface the phyllotaxis is almost exactly midway between the 2 3 and 3 5 orthogonal systems The fact that the stipular contact parastichies are expressed by appreciably lower Fibonacci numbers, i e (1 + 2), indicates the considerable tangential elongation of the primordia in this species

The result throws an interesting sidelight on certain diagrammatic representations of the primordial arrangement on the apical surface, reconstructed from careful observation of the primordial sizes and contacts (Snow & Snow 1931, figures 9, 12, 13, and 1933, figures 4, 10, 17) In these diagrams the apical surface is represented in a cylindrical transformation. In the 1931 reconstructions the resulting intersection angle of the 2- and 3-parastichies, measured on the diagrams, is 105°, and that of the 3- and 5-parastichies 61°, as the assumed divergence angle is 136°, it may be deduced from the present figure 3 that the equivalent phyllotaxis index represented by these diagrams is 2 36 Certain modifications were made in the 1933 reconstructions, and the angles of intersection of the same two parastichy pairs become 114 and 70° respectively, corresponding to an equivalent phyllotaxis index of 2 54 These numbers, especially the second, agree very closely with the value 2 5 deduced by measurement and calculation from the sections presented, and indicate the essential accuracy of the positioning of the primordia in the reconstructions of Snow & Snow, in spite of the doubts expressed by these authors as to their exactness

A final point deducible from these data refers to the rate of increase in volume of the internal apical mass in the region of initiation Calculation similar to that used in the case of *Dryopteris* leads to the conclusion that a given section in an apex having a phyllotaxis index of 3 25 will double its volume in about 1 6 plastochrones, since the plastochrone is apparently about three days, the average cell may be expected to divide every five days or rather more frequently, about four times for every division in the apical cone of *Dryopteris* in Wardlaw's experiments The assumptions underlying this result (constancy of apical size, equality of longitudinal and transverse growth rates, and absence of cell enlargement) are possibly less likely to be strictly true than in the apical cone of the fern, yet it is unlikely that any of them will lead to serious error Clearly departures from all these assumptions could be observed and some allowance made for them

(c) *Epilobium hirsutum*

One last illustration of a rather different kind may be given, again from the writings of Snow & Snow (1935) It concerns the data from an experiment in which the opposite decussate apices of *Epilobium hirsutum* were split into two by vertical diagonal cuts The majority of the regenerated half-apices subsequently developed spiral phyllotaxis, though a few either remained decussate or returned to this arrangement after a few primordia had appeared There is little resemblance between the apical patterns of opposite decussate and spiral systems, not only are their angular relations entirely different, but one of them is bijugate and orthostichous while in the other only one leaf is produced at a time and orthostichies are absent It becomes of considerable interest therefore to determine in what manner, if at all, radial spacing was affected in those apices that became spiral, and whether the relationship usually existing between the rate of growth within the *Epilobium* apex and the rate of production of primordia was modified with the pattern of the system

Drawings of one particular split apex are presented by Snow & Snow (1935, figure 11) which are of special interest from this point of view, both halves regenerated and grew well, one of them becoming spiral (Fibonacci), while the other quickly re-established the opposite decussate arrangement, at the time of sectioning the spiral apex had produced ten primordia, the other eleven Relative distances of the last six promordia from the centre in the spiral system are as follows 0 47, 0 51, 0 59, 0 78, 0 87, 1 15 By the regression method a phyllotaxis index of 3 02 is obtained This estimate is quite unchanged if the distance of the seventh leaf (1 31) also be included in the calculation, but is slightly raised (to 3 11) if either the sixth alone, or the fifth and sixth, be omitted The corresponding distances of the three youngest pairs of primordia in the opposite decussate apex are respectively 0 44, 0 63 and 0 91, and their logarithms $\bar{1}$ 643, $\bar{1}$ 799 and $\bar{1}$ 959 With only three values the best estimate of the log increment, i e that provided by the regression method, is given also from the first and third values alone Their difference, 0 316, needs to be divided by 4 in order to obtain $\log_{10} r$, for each of the two actual increments is a double one in the sense that it represents the production of two leaves Hence $\log_{10} r$ equals 0 079 and the phyllotaxis index becomes 3 01, almost identical with that obtained from the spiral partner when the same number of leaves, six, is used in each calculation If the oldest pair of leaves be omitted the resulting index is 3 05, comparing with 3 11 derived from the innermost four leaves of the spiral apex There is therefore no indication here that the phyllotaxis index was altered when the transition from an opposite decussate to Fibonacci phyllotaxis took place.

This result is confirmed by other apices figured by Snow & Snow Thus the index derived from the normal decussate apex of their figure 2 is 2 96, and those of two other apices which after cutting returned to decussation 2 94 (figure 9*a*) and 2 86 (figure 10*a*) respectively. Corresponding indices from other split apices that became spiral are 3 00 (figure 4*a*, *A*), 2 98 (figure 5*a*, *A*), 2 85 (figure 7*a*, *A*), 2 74 (figure 4*a*, *B*) and 2 72 (figure 3*a*, *A*). The last two are a little low, this may be a matter of apical size, i.e of the amount of tissue regenerating. Thus two of the specimens (figure 4*a*, *A* and *B*) were derived from a single split apex, the one with the lower index had produced only five leaves since regeneration, whereas the other had produced seven.

The general relation between phyllotaxis index and apical size may be illustrated from these same data, for in their figure 16 are presented sections of young spiral axillary buds which arose on some of the split apices when the main portion did not regenerate. The index derived from figure 16*a* is 2·68, and that from figure 16*c* is 2·29, both appreciably below the usual level in regenerated apices. Again, one axillary bud (Snow & Snow 1935, figure 17), presumably smaller than the others, produced four primordia in a distichous (alternate) arrangement, the phyllotaxis index estimated from the youngest three is 1·81. So far as the evidence goes then it appears that the transition from the alternate to the spiral system (when it occurs in these buds) may take place within the index range 1·8 to 2·3.

Returning to the full-sized regenerated apices in these experiments, the above analysis amply confirms the belief that the change from opposite decussate phyllotaxis to a spiral system has occurred without any appreciable alteration in the fundamental growth phenomena, though full confirmation perhaps requires the determination of the angle of the apical 'cone' in both types. The actual pattern on apices of the same size is to a large extent incidental. This result recalls the observation of Schuepp (1916) that the plastochrone in decussate specimens of *Helianthus annuus*, as measured between the successive leaf pairs, is double that of similar plants with spiral phyllotaxis, the plastochrone in the latter being measured in the usual way.

13. Conclusion

The primary object in the first part of this article has been to point out the inexactitude and ambiguity underlying current methods of classifying phyllotaxis patterns and to propose a new system which rigidly defines the positions of the primordia in the region of initiation by means of a numerical index (the *phyllotaxis index*) derived by simple calculation from measurements easily carried out on sectioned material. Tables also are provided in an appendix by whose use much of the calculation may be avoided.

So long as phyllotaxis at an apex is steady the measurements taken are essentially growth measurements, and these, together with the divergence angle, relate the transverse phyllotaxis pattern to the radial growth rate of the apex and to the rate at which it produces primordia; under some circumstances valuable deductions may be drawn about the rate of volume increase of the apical tissues. In spiral systems the phyllotaxis index, calculated from measurements on transverse sections, conveys information about the parastichy relations in the transverse plane much more exactly and almost as readily as does the usual method of quoting the contact parastichies of the system. For Fibonacci systems, much the most frequent of all spiral forms, these relations are immediately apparent from the index itself, for others slight extra information is required, and this also is tabulated in the appendix.

The determination of an angle on a longitudinal section, in addition to the measurements on transverse sections, further enables the phyllotaxis index to be reduced by such an amount that it now indicates the parastichy relations existing on the actual apical surface in just the same way as the original index defines those of the transverse component.

By these means phyllotaxis becomes a continuously varying function, not one which, being confined to a few discrete recognized systems, is characteristically discontinuous Phyllotaxis indices enable an important feature of all the widely different types of primordial arrangements to be quantitatively compared, with the exception of those alternate systems that arise on cylindrical apices.

The application of the methods advocated to some published data and drawings illustrates something of their scope, but more complete analyses than these might be possible on data collected specifically for the purpose, and it is hoped that the present contribution may stimulate investigations along these lines

PART II

14 EFFECT ON PHYLLOTAXIS OF CHANGING APICAL SIZE, 'AREA RATIO'

The relationship between phyllotaxis index and the transverse growth characteristics of the apex may be stated with greater precision than hitherto In the transverse system let

x = radial distance of a particular primordium at the time of its first appearance (time 0)
y = radial distance of the next primordium at the time of its first appearance (time t)
z = radial distance of the first primordium at time t
r = plastochrone ratio
c = radial relative growth rate of the apex

In the general case x need not equal y, for the central region of the apex which does not bear primordia may itself be either increasing or diminishing in size quite apart from the periodic fluctuations associated with primordium production * During the plastochrone (t) the radius x expands to z, hence

$$c=\frac{1}{t}\log_e\frac{z}{x}$$

Also

$$r=\frac{z}{y}=\frac{z}{x}-\frac{y}{x}$$

Hence

$$\log_e r=ct-\log_e\frac{y}{x},$$

or

$$\log_{10}r=\frac{ct}{2.3026}-\log_{10}\frac{y}{x}$$

$$\begin{aligned}\text{Phyllotaxis index}&=0.379-2.3925\log_{10}\log_{10}r\\&=0.379-2.3925\left[\log_{10}(ct-2.3026\log_{10}y/x)-\log_{10}2.3026\right]\\&=1.246-2.3925\log_{10}(ct-2.3026\log_{10}y/x)\end{aligned}$$

In this relation, phyllotaxis index is expressed in terms of the radial growth rate of the apex as a whole, the change in size of the bare central portion during one plastochrone, and the plastochrone itself For the practical determination of the mean change in size of the bare portion per plastochrone, and hence also c, observations of the same apex would be necessary at intervals, or alternatively it might be possible to use a sampling method; thus,

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* That large changes in apical size may sometimes occur during development is well illustrated in *Cyathea* (Wardlaw 1948), where a well-grown apex may have linear dimensions 7 to 10 times as great as those of a young apex.

when the bare apex is changing in size, growth data can be obtained only from growth measurements repeated at intervals over a period of time, although a precise relation still exists between the growth characteristics and the phyllotaxis pattern. But where the bare central apex may be assumed to remain constant in size, or its growth per plastochrone to be slight relative to the plastrochrone ratio, $\log y/x$ approaches zero and the relation reduces to

$$\text{phyllotaxis index} = 1{\cdot}246 - 2{\cdot}3925\,(\log_{10} t + \log_{10} c)$$

The radial relative growth rate c, may then be deduced from phyllotaxis measurements taken on an apex on one occasion only, provided the plastochrone is also known.

For phyllotaxis to remain constant while the bare portion of the apex is growing, $ct - 2{\cdot}3026 \log_{10} y/x$ must also remain constant. If neither the plastochrone nor the relative growth rate of the apex as a whole (c) changes, then y/x must also be invariable from one plastochrone to another. In this event the bare region expands exponentially (apart from its periodic fluctuation in each plastochrone), and calling its radial relative growth rate c',

$$\text{phyllotaxis index} = 1{\cdot}246 - 2{\cdot}3925\,[\log_{10} t + \log_{10}(c - c')]$$

It is probable, however, that the bare apical portion will increase in size more nearly linearly, so that y/x, and therefore c', decreases with time. Under these conditions phyllotaxis index also decreases. If both the growth rate of an apex as a whole and the plastochrone remain constant, while the central bare area increases from a previously fixed size until it reaches another at which it again becomes stable, the phyllotaxis index during the change must first rise from its initial value to a higher one and finally fall again to the original value. The change in size of the apex will have had a temporary effect on phyllotaxis (while it was occurring), but no permanent effect. In fact, however, the height of phyllotaxis is known usually to be correlated with size of apex, hence it appears inevitable that, when the bare portion increases in diameter, either the growth rate of the apex as a whole, or else the plastochrone, must normally diminish. Presumably the dominant effect is on the plastochrone, and indeed such a change may almost be regarded as automatic, as the following considerations show.

Whatever may be the immediate causes of the *absolute* distancing of the primordia from one another at initiation, assume that they do not change while the radius of the bare portion of the apex producing them increases from R_1 to R_2, provided that full contact is maintained among the primordia, this is tantamount to the assumption that their absolute size at initiation does not alter with that of the bare region of the apex. Assume further that the relative growth rate of the whole apex, c, does not alter. Primordia are produced, both before and after the change in apical size, as rapidly as space becomes available, through growth of the system, beyond the limit defined by the circle of radius R_1 (or R_2). The rate of liberation of space beyond such a circle depends on (1) the circumference of the circle and (2) the rate of recession of the newly formed primordia from its vicinity, due to apical growth. Since the apex is assumed always to expand exponentially at the rate c, each of these factors is proportional to R, and when the bare apex changes its radius from R_1 to R_2 the rate of liberation of space available for primordium production becomes $(R_2/R_1)^2$ times the original rate. Hence the plastochrone changes in the inverse ratio.

Since phyllotaxis index equals $1{\cdot}246 - 2{\cdot}3925\,(\log_{10} t + \log_{10} c)$, it must decrease by $2{\cdot}3925 \log_{10} (R_1/R_2)^2$, i.e. increase by $4{\cdot}785 \log_{10} R_2/R_1$. If then no changes occur in the magnitudes of the factors concerned in the distancing from one another of the primordia at initiation, and the diameter of the bare apex doubles, phyllotaxis index automatically increases by 4 785 $\log_{10}2$, or 1 44 units, for a rise of one unit due to this cause the apical diameter must increase to 1 618 , i e $\frac{\sqrt{5}+1}{2}$ times its original length, or its area to 2 618 or $\frac{\sqrt{5}+3}{2}$ times the initial size

The concept of phyllotaxis index as a resultant of the transverse apical growth rate and of the plastochrone thus leads easily to another, equivalent to that of 'bulk-ratio', i e the relative sizes of apex and primordium in relation to phyllotaxis level In the present terms the relation is particularly simple, for it is evident that although the method of approach has been to postulate a constant primordial size, or rather spacing, and varying apical size, yet it is the ratio of the two that determines the phyllotaxis index, the absolute sizes of apex and primordium are immaterial, and provided their ratio is constant phyllotaxis also is fixed Hence, as regards the transverse component of the system, a change of 2 618 times in the ratio of bare apical area to the area associated with a newly initiated primordium leads always to a change of one unit in the phyllotaxis index, regardless of whether the change occurs in apical size alone, primordial size alone, or in both simultaneously

The solution of the problem of 'bulk-ratio' given here is, moreover, a practical one, being in a form in which it may easily be applied to the plant This is so because elements have been chosen that are unaffected by the idiosyncrasies of particular apices, e g the shapes of primordia are not considered It should be emphasized also that it is not necessarily the transverse area of the newly initiated primordium that is referred to, but the projection on a transverse plane of the portion of apical surface associated with a single primordium, whether or not the whole of that area is actually occupied, it is the maximal possible transverse size of a primordium that can exist without compression in the particular phyllotaxis pattern This definition of 'primordial area' should be borne in mind throughout the following pages

A practical illustration may help to clarify one manner in which the relationships between apical size, primordial spacing and phyllotaxis may be investigated Church (1904, figures 40 and 41) presents drawings depicting transverse sections of four apices of *Araucaria excelsa*, these differing in their phyllotaxis systems and apical diameters A similar set of drawings from four apices of *Podocarpus japonica* is presented in his figure 42, and a third set from four apices of *Lycopodium Selago* in his figures 78 and 79 The drawings for any one species are to the same scale of magnification, but this evidently does not hold between the different species, though the actual scales are not stated The phyllotaxis types are widely divergent, according to Church's method of classifying them, three of the *Araucaria* apices show Fibonacci systems· (3+5), (5+8) and (8+13), the fourth being of the first accessory type, (7+11) In *Podocarpus* two are Fibonacci, (3+5) and (5+8), one first accessory, (3+4), and the fourth Fibonacci bijugate, (6+10), while in *Lycopodium* there are two systems of alternating whorls, (4+4) and (5+5), and one from each of the second and third accessory types, i e (4+5) and (5+6)

From measurements made on any one of these drawings, and involving only a few of the innermost primordia, the phyllotaxis index may be calculated, using the regression method (see p. 541) on the logs of the radial distances of the successive primordial centres P_1, P_2,

P_3, Thus from the (8+13) *Araucaria* apex has been obtained the regression equation $Y=0·01085P+0·844$, where P is the number given to any primordium and Y is the predicted value for the logarithm of its radial distance (in mm., as measured on the drawing), 0·01085 is $\log_{10} r$, and from it the phyllotaxis index is calculated as 5·08. If now the 'bare apex' is defined as that region on which primordial *centres* do not arise (the distances of the primordia being measured to these centres), the best estimate of the logarithm of its radius is obtained from the value of Y in the regression equation when P is made equal to 0·5, i.e. 0·849. The reason for this is that in the drawings of Church the stage in the plastochrone is quite unknown, one can only assume a random distribution of the stage among them and that on the average the mean will be the mid-plastochrone. The position of P_1 one-half a plastochrone earlier than appears in the drawing is thus required, and is obtained by putting $P=0·5$.

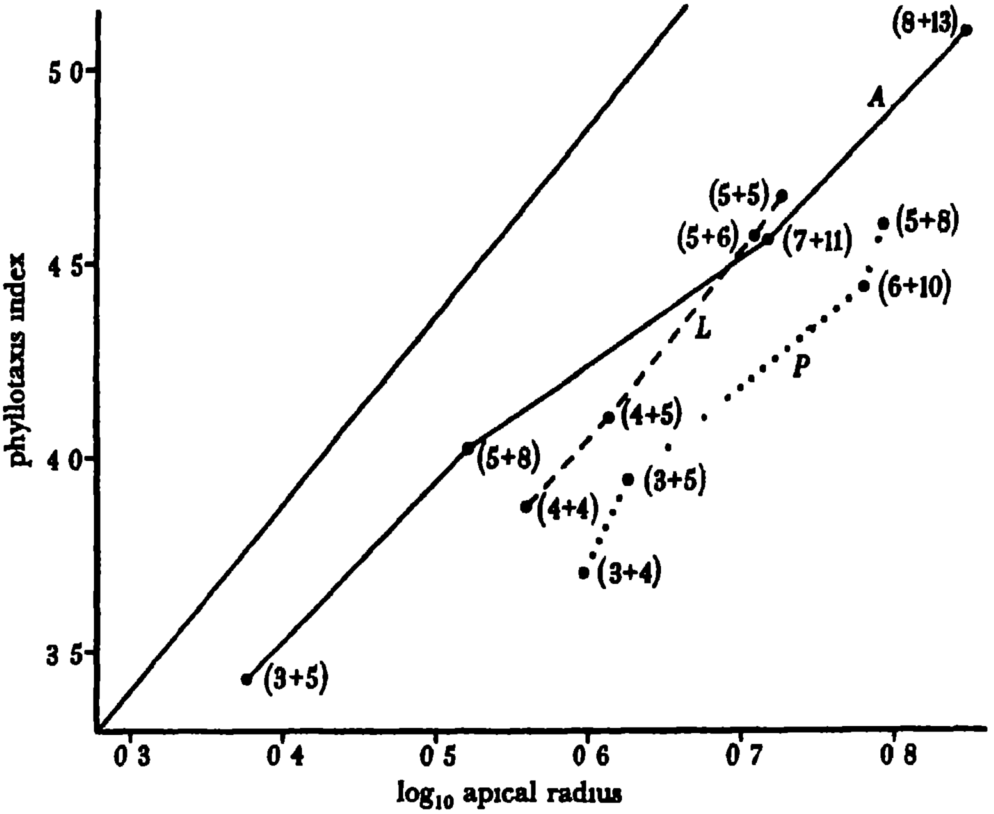

FIGURE 7. Relation between phyllotaxis index and the logarithm of the radius of the bare apex. Primary data taken from Church (1904). *A*, *Araucaria excelsa*, *L*, *Lycopodium Selago*, *P*, *Podocarpus japonica*. The straight line shows the slope of the relationship if primordial size is constant.

In figure 7 the two calculated quantities, phyllotaxis index and log apical radius, are plotted against one another, both for this apex and also for the other three of *Araucaria* depicted by Church. The four points are connected by straight lines (*A*). The similar relation between the four *Podocarpus* apices is also shown (*P*), together with that in *Lycopodium* (*L*).

Some difficulty arises in the treatment of the two whorled apices of *Lycopodium*; in the (5+5), for instance, five primordia are produced together. The procedure adopted here is to determine the mean log radial distances in each of the youngest two whorls, 0·768 and

0·849 respectively. $\log_{10} r$ (corrected) is obtained by dividing the difference between these two quantities by five, giving 0·0162, and hence a phyllotaxis index of 4·66. The mean of the log distances in the two whorls is also required, i.e. 0·808, together with the mean 'primordium number'. Calling those in the youngest whorl 1, 2, 3, 4 and 5 respectively, and those in the next whorl 6–10, the mean number becomes 5·5. A conventionalized regression equation may now be set up $Y-0·808=0·0162\,(P-5·5)$, or $Y=0·0162P+0·719$. Putting $P=0·5$ again gives the best estimate of log apical radius (0·727), and this value is plotted in figure 7.

By these means the apex is treated as if it were unijugate, producing the ten primordia one at a time in uniform succession instead of in two whorls. Putting $P=3$ in the regression equation reproduces the actual mean log distance in the innnermost whorl, while if $P=8$ that in the second whorl is produced. When $P=-2$ an estimate of the actual present radial distance of the centres of the next whorl to be produced ($P=0$, -1, -2, -3 and -4) is obtained. According to the convention of unijugy therefore it is known that primordium 3 has already appeared and that primordium -2 has not yet done so, nothing is known of the conventional presence or absence of the four intermediate primordia, but in a number of such apices on the average numbers 2 and 1 would have appeared but not numbers 0 and -1, the mean stage being again 'mid-plastochrone' between numbers 0 and 1. Hence to obtain the estimate of log apical radius comparable with that from the truly unijugate apices, P in the equation is taken equal to 0·5. The average error may be larger than in unijugy, but is unbiased, the actual agreement in figure 7 between the points representing the two whorled apices of *Lycopodium* and those calculated in a more standard manner from spiral apices is strikingly good.

Since all the drawings for any one species are to the same scale, if the absolute spacing of the primordia in them is similar then a line through the four points plotted will represent simply the effect of varying apical size on phyllotaxis, as discussed above. The line must then have a slope equal to the reciprocal of $\log_{10} 1·6180$, or 4·785 (i.e. the same slope as the best line through the points in figure 6). If the slope has a different magnitude the departure indicates a change in primordial spacing (or in the linear dimensions of the primordia if full contact be assumed) accompanying the known difference in apical size. A line of the theoretical slope has been drawn in figure 7, and it may be seen at once that the data derived from the *Lycopodium* apices agree remarkably well with it, those for *Podocarpus*, though a little irregular, possibly indicate a slightly different slope. The data of *Araucaria* display a slope which appears to be probably different, though not very greatly so, from that to be expected if apical size were its sole determinant. If lines of theoretical slope were drawn through the two extreme points in this species, representing the largest and smallest apices, they would be separated horizontally by a distance equivalent to $\log_{10} 0·129$. If this is accepted as real it implies that the assumption of uniform primordial spacing does not hold, but that the primordia in the (8+13) contact system are about 1·35 times as far apart at initiation as those in the (3+5) system, and probably therefore that the larger apex produced primordia which from the start were larger than those on the smaller apex. This difference in size, however, is not very great compared with that between the bare apices, whose diameters are in the approximate ratio 3 : 1. Needless to say, it is quite impossible to determine directly from the original drawings whether or not the size of the ill-defined youngest primordium varies with apical diameter, and owing to very different amounts of growth per plastochrone in the various phyllotaxis systems older primordia cannot be directly compared

The relation between phyllotaxis index and the ratio of the transverse area of the bare apex to the maximum possible transverse primordial area at initiation may readily be expressed in a more concrete form In discussing this relation the assumption will again be made that any change in size of the bare apex from one plastochrone to another is sufficiently small to be negligible When it is not so, plastochrone ratio and phyllotaxis are likely to be changing rapidly and conditions are then unsuited to any simple practical analysis In the first place it should be stated that in the transverse component of a constant phyllotaxis system the outline of the bare portion of an apex is not circular and may be complex in form, the apex nevertheless has a shape that is maintained It may be regarded as expanding uniformly during the plastochrone to its maximum size and then surrendering a certain amount of its area, again of definite form, to a primordium The bare apex is now at its minimum size, but it has precisely the same shape as before,* the new figure being orientated differently from the original, in a Fibonacci system it is rotated through the Fibonacci angle, etc Hence the piece of apex associated with the primordium is in the nature of a geometrical gnomon to the bare apex A figure of a certain shape, and having a particular linear dimension of unity, say, expands uniformly until the corresponding measurement is r (the plastochrone ratio), it then parts with a gnomon, leaving its shape unaltered but reducing it to the original dimensions The maximum and minimum figures, being geometrically similar, have areas proportional to the squares of equivalent dimensions, i e $\frac{\text{minimum area}}{\text{maximum area}} = \frac{1}{r^2}$ The ratio of the maximum apical area to the area of the primordium at initiation is $\frac{r^2}{r^2-1}$, and that of the minimum apical area to the primordial area $\frac{1}{r^2-1}$

Every value of r corresponds to a particular phyllotaxis index, hence the relation between this index and the ratio of either maximum or minimum apical area to primordial area may readily be calculated The two relations are shown respectively in *A* and *B*, figure 8, but phyllotaxis index is plotted there against the logarithms of the ratios to base 10 At low indices the two curves diverge widely, but as phyllotaxis rises they rapidly approach the same straight line, for here the fluctuations in apical size are very small and it becomes immaterial at what stage in the plastochrone the area is considered The actual values for the ratio of maximum apical size to primordial size in the various orthogonal Fibonacci systems have been tabulated in an earlier paper (Richards 1948) in the form $\frac{100(r^2-1)}{r^2}$, i e the percentage of the cross-sectional area of the enlarged smooth apex associated with a single primordium at initiation

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* This may not always be true, and the bare apex, in the above sense of the term (as distinct from the visibly bare apex) may actually change its form during the plastochrone It may readily be shown, however, that even so all the area relations deduced in the following paragraphs remain unchanged for all practical purposes, though the *precise* mathematical form and position of the lines *C* and *D* in figure 8 become theoretically uncertain

Curve C in figure 8 gives the phyllotaxis index in relation to the ratio of apical size at mid-plastochrone to primordial area at initiation; it is more nearly linear than the other two At this time any dimension of the apex has a magnitude equal to the geometric mean between its extreme values, hence the curve plotted is the log of $\frac{r}{r^2-1}$ Finally, the straight

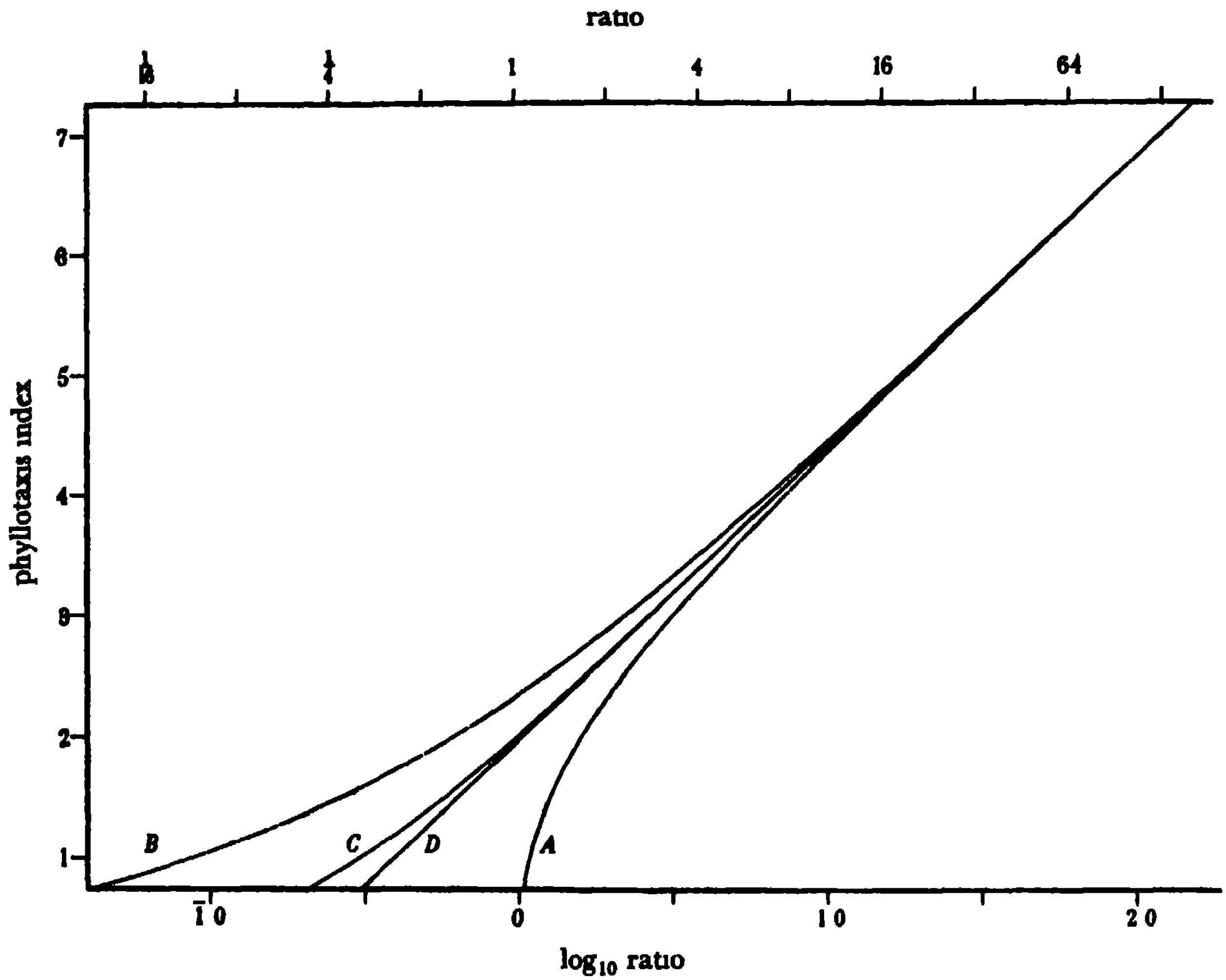

FIGURE 8 Relation between phyllotaxis index and the logarithm of the ratio of bare apical transverse area to the transverse area associated with a single primordium A, the relationship when maximum apical area is considered, B, that for minimal apical area, C, that for apical area at mid-plastochrone, and D, that for mean apical area, i e the 'area ratio'

line D on the diagram gives the corresponding relation when the apical area considered is the true mean area For in a system expanding exponentially from radius = 1 to radius = r, the mean area is given by the ratio of the difference between the extreme areas to the difference between their natural logarithms, i e mean apical area is proportional to

$$\frac{r^2-1}{\log_e r^2 - \log_e 1} = \frac{r^2-1}{2\log_e r}$$

Since primordial area is similarly proportional to r^2-1, the ratio of mean apical area to primordial area $= \frac{1}{2\log_e r}$ In any phyllotaxis system, this quantity $\frac{1}{2\log_e r}$ will be termed the *area ratio*, it will be seen to be the reciprocal of the relative growth rate in transverse area of the apex when time is measured in plastochrones. In *D*, figure 8, therefore, phyllotaxis index is plotted against the logarithm to base 10 of the reciprocal of $2\log_e r$, or $\log_{10}\left(\frac{0\cdot21715}{\log_{10} r}\right) = -0\cdot6632 - \log_{10}\log_{10} r$. Since phyllotaxis index $= 0\cdot379 - 2\cdot3925 \log_{10}\log_{10} r$ the relation plotted is rectilinear, with the slope 2·3925 (straight line *D*).

This slope is one-half that of the theoretical line on the previous figure, and as the latter gives a relation in terms of linear dimensions and the former in terms of area, the two clearly refer to the same conditions, that is to say, the apical radius appropriate to the theoretical line in figure 7, derived from considerations of rate of availability of space for primordium formation, is the radius corresponding to the mean area during the plastochrone. Figure 8 shows that for phyllotaxis indices of the magnitudes actually investigated, 3·4 and upwards, the particular time in the plastochrone at which the apex is measured is not of great moment, since the curves for both maximum and minimum apical size depart relatively little from that for mean size, but, as will be readily appreciated from the diagram, investigations of this nature involving apices having much lower phyllotaxis indices would need to have special attention paid to this aspect. Again, at the level of phyllotaxis index under investigation the line on figure 8 representing the relation with apical area at mid-plastochrone is indistinguishable from the straight line representing the relation with mean apical area, this latter is the theoretical comparison line actually used in figure 7, but strictly the mid-plastochrone relationship should have been used.

So far, in dealing with the figures of Church, estimates have been obtained of the transverse size of that portion of the apex on which primordial centres do not arise (or of the radial distance at which these centres arise), and of the relative initial sizes of the primordia in the several specimens from one species. Estimates of the absolute sizes of these primordia at the time of their initiation, as defined on p. 549, may also be made from figure 7, for the theoretical line there has been drawn to correspond with that of *D*, figure 8, not only in slope but also in position, the horizontal reading at any phyllotaxis index in the former being numerically one-half that in the latter. Hence, assuming the primordial area to be replaced by an equal circle (of radius R_p), for any phyllotaxis index the line drawn in figure 7 gives $\log_{10}\left(\frac{\text{apical radius}}{R_p}\right)$, i.e. $\log_{10}$ apical radius $-\log_{10} R_p$. Since the point calculated from any particular apex gives $\log_{10}$ apical radius, the horizontal distance between the point and the line must represent $\log_{10} R_p$, the logarithm of the radius of the circle equal to the area on the original section associated with a primordium at initiation, measured in the same units as the bare apex, in this case mm. on Church's drawing. The actual transverse area associated with a primordium at initiation may thus be obtained, as represented on the original drawing.

Applying this to the points in the diagram representing the (8+13) and (3+5) apices of *Araucaria*, horizontal distances of 0·198 and 0·069 respectively are found, leading to estimates of the primordial areas of 7·8 and 4·3 sq. mm. Similar calculations starting from the values for $\log_{10}$ apical radius on the graph, or in the primary regression equations, lead to mean apical areas of 156 and 17·7 sq. mm. respectively. Consequently the ratios of these areas, i.e. the 'area ratios', in the two apices are 20·0 and 4·12; their logarithms are

1 301 and 0 615, which when plotted in figure 8 against the phyllotaxis indices of the apices, 5 08 and 3·43 respectively, fall on the theoretical straight line there

The implications involved in such calculations should be carefully considered, since the values obtained depend on the postulates inherent in the methods used for their evaluation In the present example the radial distances of the primordia were originally measured from their geometrical centres, and the regression calculation employed led to the determination of two numerical constants, one of them being the plastochrone ratio From these constants the radial distance of the primordial centres at the time of their first appearance was estimated, by so doing it was implied solely that the apex may be supposed continually to be expanding past the circumference of a *fixed* circle, which serves merely to indicate at any time the region where new primordial centres appear

In using this same circle as one of the two parameters from which primordial size at initiation is to be estimated, however, it is regarded in a very different manner, as representing the *mean area* of an apex pulsating rhythmically in the period of the plastochrone Underlying the method lies the conventional postulate that the bare apex expands exponentially, when a certain maximum size is attained a primordium is instantaneously 'initiated', reducing the bare apex once more to its minimum size One may define how one pleases the size of the circle to represent the mean area of the apex, but once this is defined the 'primordial area' is automatically defined also, for in the analysis it is completely determined by the mean apical area and the phyllotaxis index In the present case the area taken to represent the 'bare' apex at its mean size is that circle on whose circumference the geometrical centres of the primordia make their first appearance, so that when the apex is regarded as pulsating in size the circumference of an equal fluctuating circle may be supposed to lie inside the line of appearance of primordial centres at the beginning of the plastochrone and outside it at the end, while its position when the apex is at its mean size defines the line The annulus between the limiting positions has then, to a reasonable approximation, the same area as that associated with each primordium at the time of its appearance, whether the primordia are actually annular or of any other form, the chief practical difficulty lies in the precise location of the primordial 'centres' in any particular case, so that the measurements taken may conform to the demands of the theory

Approached in this way, the time of 'initiation' of the primordium, as well as the apical area associated with it at this time, is conventional, being governed by the definition of size we choose to give to the 'bare' apex If, however, the time of initiation be defined by other criteria (such as the time of leaf 'determination' in the sense of the word as used by Snow & Snow (1931) measured in plastochrones before the appearance of the hummock, or the time of the first periclinal divisions), then the corresponding apical radius would be obtained by substituting the appropriate value, instead of 0 5, for P in the regression equation on p 550 The absolute area associated with the primordium at this defined initiation time could then be evaluated The estimate of the ratio of mean apical area to primordial area is of course unaffected by the particular definition given to either the time of primordial initiation or the 'bare' apical area, since it depends solely on the phyllotaxis index

Before leaving figure 7 attention may once again be drawn to the classification of the apices by Church according to the numbers of contact parastichies In general, as would be expected, phyllotaxis index rises with the numbers of contact parastichies, but there are notable exceptions. In *Podocarpus*, for instance, a (5+8) apex appears above a (6+10), or again, the (7+11) *Araucaria* apex has the same index as the (5+6) *Lycopodium* apex, and apparently a lower one than even the (5+5). These discrepancies arise, of course, from the fact that the contact parastichies in the various apices intersect at very different angles, and hence do not really indicate the 'bulk-ratios', as Church assumed. The area ratio on the other hand is a direct measure of precisely this kind and its logarithm is linearly related to the phyllotaxis index, when the transverse component of the system is alone under consideration, i.e.

$$\log_{10} \text{area ratio} = \frac{\text{phyllotaxis index} - 1\cdot 9660}{2\cdot 3925}.$$

With the aid of a table of natural logarithms it may be obtained even more simply from the plastochrone ratio, as the reciprocal of $2 \log_e r$.*

15. AREA RELATIONS INVOLVING THE APICAL SURFACE

Theoretical measures such as bulk ratio, which depend for their validity on some defined and simple primordium shape, fail when the attempt is made to apply them to actual apices, where the primordia are of differing and uncertain forms. They also fail in fern apices, at least, for another reason, that the primordia do not nearly fully occupy the apical space they control. The area ratio on the contrary may readily be estimated on an apex and provides information of precisely the kind sought, quite regardless of the actual primordium size and shape.

But while the information derivable from the relationship between phyllotaxis and the area ratio applies only to the transverse component of the system, it may be desired to extend an investigation of a similar nature to the whole three-dimensional system. For this purpose an equation is required relating the equivalent phyllotaxis index to the actual primordial area on the apical surface and some determinable area characteristic of the bare apex (by 'primordial area' is meant here, and in what follows, the *apical* surface area associated with a single primordium at initiation, not the surface area of the primordium).

It would be possible to deduce such a relationship using the bare apical surface area as the third of these variables, provided the apex was assumed always to conform to some specified shape, a paraboloid for instance. This procedure, however, would immediately be open to a similar criticism to that just raised against the concept bulk-ratio, for the form of apices is unknown and very variable, and serious errors might be involved in the attempt to apply the resulting relationship to actual phyllotaxis systems. No similar objection arises if the transverse area of the bare apex, in the region of primordial initiation, be substituted in the relation for the apical surface area: that is to say, the same area that has already been considered in the area ratio Moreover, it will be clear from the sequel that the only way in which the shape of the whole apex affects geometrically the height of phyllotaxis is through this transverse area in the region of leaf initiation Hence in what follows the equivalent phyllotaxis index will be related to the ratio between the transverse apical area and the actual primordial area on the apical surface

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* The area ratio calculated in this way for a multijugate apex is no more conventional in character than that derived from a unijugate apex. For in an x-jugate system let r_a be the actual ratio of the radial distances of the primordia in two successive whorls, and r the conventional plastochrone ratio as used above, so that $\log r_a = x \log r$. The actual maximum apical area is proportional to r_a^2, and the actual minimal area to 1, hence the actual mean apical area is $\dfrac{r_a^2 - 1}{2 \log_e r_a}$. The area given over to x equal primordia at initiation is similarly proportional to $r_a^2 - 1$, hence that of each primordium is $\dfrac{r_a^2 - 1}{x}$. The actual ratio of mean apical area to primordial area is therefore $\dfrac{x}{2 \log_e r_a} = \dfrac{x}{2x \log_e r} = \dfrac{1}{2 \log_e r}$.

For this purpose the relation between the actual primordial area on the apex and its transverse component is required A closely approximate solution to this problem may be arrived at by again imagining a cone to be fitted tangentially to the apex in the region of initiation of primordial centres, the cone having an angle of 2θ The outline of the area representing a primordium on the apical surface may then be projected on to the conical surface Since in the region of primordial initiation the cone and apex are almost in contact at all relevant points, the area of the projection on the cone will reproduce with considerable accuracy that of the primordium on the apex If now this area on the cone be itself projected orthogonally on to a transverse plane, the area of the transverse projection is $\sin\theta$ times that of the projection on the cone, it therefore closely approximates $\sin\theta$ times the actual primordial area

This relation is, of course, not strictly accurate, since it again is affected slightly by the form of the apex, nevertheless it is evident that the error involved in accepting it will be inappreciable practically, except possibly in extremely low phyllotaxis systems wherein the primordial area is large relative to the apex

The relation given on p 556 between phyllotaxis index and area ratio may be expressed

$$\text{phyllotaxis index} = 1\ 966 + 2\ 3925\ (\log_{10} \text{transverse apical area} - \log_{10} \text{transverse primordial area})$$

Now, equivalent phyllotaxis index = phyllotaxis index $+ 2\ 3925 \log_{10} \sin\theta$
Therefore

$$\text{equivalent phyllotaxis index} = 1\ 966 + 2\ 3925\ (\log_{10} \text{transverse apical area} - \log_{10} \text{transverse primordial area} + \log_{10} \sin\theta)$$

But transverse primordial area = actual primordial area on apex $\times \sin\theta$,

or $\log_{10}$ transverse primordial area $= \log_{10}$ actual primordial area $+ \log_{10} \sin\theta$

Therefore

$$\text{equivalent phyllotaxis index} = 1\ 966 + 2\ 3925\ (\log_{10} \text{transverse apical area} - \log_{10} \text{actual primordial area}),$$

and

$$\text{phyllotaxis index} = 1\ 966 + 2\ 3925\ (\log_{10} \text{transverse apical area} - \log_{10} \text{actual primordial area} - \log_{10} \sin\theta)$$

The first of these two final relations is similar to that on p 556 between area ratio and phyllotaxis index, but it is now the *equivalent* phyllotaxis index and the primordial area *on the apex* that are referred to The range of applicability of figure 8 may therefore be extended to include the more general relation An analysis of the immediate causes of changing phyllotaxis on the surface of growing shoot apices, for example, could thus be made, using only measurements easily taken from transverse and longitudinal sections At each growth stage investigated the regression method as used in the analysis of Church's drawings would enable the estimates of $\log_{10}R$ (apical radius), $\log_{10}r$ and phyllotaxis index to be obtained from a transverse section, θ may be directly measured on a longitudinal section and by its use the index converted into equivalent phyllotaxis index Log$_{10}$ apical transverse area is given by $2\log_{10}R+0\ 4971$, and log$_{10}$ primordial area may then be obtained from the equation, or alternatively from the formula * $1\ 1604+2\log_{10}R+\log_{10}\log_{10}r-\log_{10}\sin\theta$ Hence any modification occurring with age, etc, in the equivalent phyllotaxis index might be interpreted as the resultant of two numerically defined changes due to the alterations which have occurred respectively in the absolute distancing of the primordial centres from one another on the apical surface and in the transverse size of the apex in the region of initiation Any modification of the phyllotaxis index is a resultant of these same two changes plus a third due to alteration in the form of the apex in the same region (the angle θ)

It is noteworthy that for any given transverse apical area and primordial area the equivalent phyllotaxis index is independent of the angle θ and apical shape, for any given divergence angle the parastichy intersection angles near the region of initiation on the surfaces of all apices, whether elongated or flat, are identical provided the ratio of primordial area to mean apical transverse area is the same As a point of theoretical interest, since the curve system is independent of the angle θ, the above relation holds even for cylindrical structures such as are found in many Gramineous apices The application of the equation also to the phyllotaxis curves seen in many mature structures, where flowers or fruits are crowded together round an axis which is a surface of revolution, will be apparent, here the phyllotaxis curves in any region are determined solely by the divergence angle, the area occupied by a single fruit and the transverse area of the whole structure in that region the actual shapes of the fruits are immaterial to the parastichy systems, though they will of course help to determine which of these curves represent the *contact* system

16 RECAPITULATION AND GENERAL VALIDITY OF THE PROPOSED METHODS

In the preceding pages phyllotaxis index has been expressed in very different ways It was originally defined as a simple transformation of the plastochrone ratio, a measure that may readily be obtained from a transverse section of the apex, for the purpose of defining the radial component of phyllotaxis in a manner which, given also a knowledge of divergence angle, supplies immediate information as to the parastichy relations to be seen in the section Plastochrone ratio, while easily measured and readily understood in relation to

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* This is derived as follows

$$\frac{\text{mean transverse apical area}}{\text{primordial area in transverse projection}}=\text{area ratio}=\frac{1}{2\log_e r}$$

Therefore

$$\frac{\text{mean transverse apical area}}{\text{primordial area on apical surface}}=\frac{\sin\theta}{2\log_e r}$$

Denoting the apical radius, when the apex is at its mean transverse area, by R, it follows immediately that the actual primordial area equals $\frac{2\pi R^2\log_e r}{\sin\theta}$ or $14\ 47\ R^2\log_{10}r\ \mathrm{cosec}\,\theta$, whose logarithm appears above In a flat apex, or in the transverse component of any apex, $\mathrm{cosec}\,\theta=1$, and the resulting formula thus allows the primordial areas in the sections already considered, from Church, to be calculated directly from the two constants in the fitted regression equation a section across the apex, is not necessarily a simple concept when considered in relation to the processes of growth and differentiation in the apex It may be compounded of the rates of three simultaneously occurring processes rate of production of primordia, overall rate of transverse growth of the apex in the region of the youngest primordia, and rate of change in transverse size of that apical region inside the zone of primordial initiation Change in any one of these three rates is reflected in a corresponding alteration of the phyllotaxis index, the relation of the latter to the three processes is given on pp. 547–548 Phyllotaxis index may then be expressed entirely in terms of rates of change within the apex, and, if desired, even calculated from these, i e from dynamical physiological considerations only

As a result of the various growth processes the ratio between the sizes, in the transverse direction, of the apex itself and the portion of it associated with a single primordium at initiation attains a particular magnitude in a certain time Provided the various rates are so correlated that the area ratio remains substantially constant for a period, the parastichy curves also remain constant in form, and the phyllotaxis index is rigidly and simply related to the ratio, i e the index is now expressed entirely in static morphological terms (p 556) Even if the areas considered are changing differentially in time the phyllotaxis index corresponding to any particular plastochrone may, theoretically at least, be determined (see later, p 560), but it can no longer be regarded as a constant and phyllotaxis is variable Phyllotaxis index and plastochrone ratio therefore are concepts related equally to the morphology of the shoot apex and to certain rates of growth and differentiation within it

By a slight extension of the morphological analysis the height of phyllotaxis on the apical surface itself may be shown to be completely defined by the ratio of apical cross-sectional area to the amount of apical surface associated with a single primordium, in just the same way as the phyllotaxis in the transverse component is defined by the area ratio (p 557)

The questions discussed in the foregoing pages, and the validity of the analytical methods developed, are not directly concerned with those aspects of phyllotaxis theory that relate to the immediate physiological causes underlying the emergence of a primordium at a particular place on the apical dome Only the well-known regularities in both tangential and radial spacing due to these causes have been accepted as facts of observation, and certain relationships which must necessarily follow have been investigated Theories of the underlying causes of phyllotaxis, if they are to account for all the factors recognized here as contributing to the geometrical pattern produced, must explain (1) the absolute distancing of the primordial centres from one another, usually regarded as a consequence of the influence of existing primordia in determining the position of the next one to appear, and (2) the absence of primordia from the central apical dome and the factors determining its transverse size in the region of initiation Since the phenomena of phyllotaxis may be discussed also in terms of growth rates within the apex, an ideal theory would be capable, under clause (2), of accounting for the plastochrone in relation to these rates The reasons for the appearance of the various 'ideal angles' in apices will be answered implicitly under clause (1) above, but a full understanding of radial spacing and phyllotaxis index requires the explanation of both groups of phenomena A few aspects of phyllotaxis may fall under neither of these headings, e g the tendency of some apices to maintain or establish whorled constructions under apparently adverse conditions (cf Schoute 1922, 1925, 1936, 1938, Snow 1942)

Whatever the ultimate solution of these problems may be, the applicability of the analytical methods proposed will remain unaffected At first sight they appear to rest on two assumptions uniformity of tangential primordial spacing and constancy of plastochrone ratio as measured on sections from the successive pairs of primordia. Only if both these are true will the parastichies as seen in transverse projection be logarithmic spirals, and these curves have been used in the establishment of the theoretical relation between parastichy intersection angle and plastochrone ratio, and hence also phyllotaxis index

The approximate regularity in tangential spacing, and the apparently extraordinary exactness with which the mean divergence angle may approach particular irrational values, have long been recognized as facts, at least in the vast majority of plants, and studies in leaf arrangement from the first have been stimulated by these phenomena, and largely confined to them The second assumption, constancy of the plastochrone ratio, might on the contrary legitimately be questioned, and with it therefore the description of the parastichies as *logarithmic* spirals As d'Arcy Thompson (1942, p 918) states, 'the curves resemble, and sometimes closely resemble, the logarithmic spiral, but that they are, strictly speaking, logarithmic is neither proved nor capable of proof', and again (p 914), 'They doubtless resemble the logarithmic or equiangular spiral, but different spirals may look much alike, and these are ill-suited to the careful admeasurement and rigorous verification which Moseley gave to the spirals of his molluscan shells '

In the first place, when estimates are made of the transverse distances of the successive primordia from the apical centre, the logarithms of these distances are never exactly in arithmetical progression, the ratio between each pair of successive distances fluctuates, so that there is a greater or lesser amount of 'random' error in the radial positioning In order to obtain the best estimate of the increment in log distance corresponding to a single plastochrone a regression must be fitted to the data If the observed log distances are reproduced adequately by a rectilinear relation, there being no statistical evidence that a curved regression will fit them appreciably better, then the original assumption is justified and the smoothed or idealized parastichy lines may be taken as logarithmic spirals within the limits of accuracy set by the random fluctuations So long as measurements are confined to only a few of the inner primordial cycles on an apex these conditions are usually found to apply, and the subsequent calculations then clearly give the correct relation between phyllotaxis index and parastichy intersection angle

But when older zones of primordia are included in the investigation the assumption of a constant proportional increase in axis diameter with primordium number is no longer found to hold, and a curved regression fits the log distances better than any straight line Sometimes evidence of curvature in the relationship may be found even in the inner zones In such circumstances the assumption of logarithmic spiral parastichy lines is certainly unjustified, nevertheless from an appropriate curved regression estimates of the plastochrone ratios (no longer constant) may be obtained corresponding to any particular zones of primordia on the apex, and from these the changes in phyllotaxis index followed from the centre outwards If for instance the regression is put in the form $Y=a+bP+cP^2$, where Y is the estimated log distance of primordium number P, and a, b and c are constants, the slope of the regression is $b+2cP$, by putting in this expression $P=5$, for example, the estimate of $\log r$ is obtained for a narrow annulus on the apex containing the fifth primordium

Phyllotaxis is thus changing with distance from the apical centre, but the phyllotaxis index for a particular zone, as calculated from the curved regression, still indicates the parastichy intersection angle in that region For the short segments of the parastichy lines in each zone may be regarded in essence as having been replaced by closely fitting bits of logarithmic spirals, and the complete parastichies as built up of a large number of segments taken from different logarithmic spirals The intersection angles of these theoretical curves will therefore agree everywhere with those of the actual parastichies within the limits of accuracy permitted by the random irregularities of the latter, and are correctly indicated at any position by the calculated phyllotaxis index Hence, so far as the analytical methods are concerned, the precise form of the spiral parastichies is of no moment

The survey of methods for defining the positions of primordia near the apex, as developed in these pages, has shown increasingly the significance attaching to their radial and longitudinal positioning, in many ways the tangential spacing is of less immediate interest and usefulness, yet it is this latter aspect that has engaged almost exclusively the attention of botanists This *lacuna*, which phyllotaxis index is designed to fill, was noted by d'Arcy Thompson (1942, p 917) who, in focusing attention on the importance of longitudinal spacing in phyllotaxis patterns, wrote 'But this matter botanical students have not concerned themselves with, in other words, their studies have been limited (or mainly limited) to the relation of the leaves to one another in *azimuth*—in other words, to the angle ϕ [the divergence] and its multiples' A paper like the present, intimately concerned with questions of the interrelationships between form and growth, cannot end more fittingly than with this reproof from so eminent an exponent of many such problems

APPENDIX

A 1 *Phyllotaxis indices at orthogonal intersection in the successive systems for various 'ideal' divergence angles*

angle	137 50776°		99 50155°		77 95525°		64 07936°		151 13566°	
	system	index	system	index	system	index	system	index	system	index
	1 2	0 95	3 4	2 71	4 5	3 23	5 6	3 65	5 7	3 84
	2 3	2 02	4 7	3 65	5 9	4 15	6 11	4 56	7 12	4 79
	3 5	2 99	7 11	4 68	9 14	5 19	11 17	5 60	12 19	5 81
	5 8	4 00	11 18	5 67	14 23	6 18	17 28	6 58	19 31	6 80
higher systems		*x* 00		*x*·67		*x* 18		*x* 59		*x* 80

A 2 *Multijugate systems*

The index for orthogonal intersection in the *x*-jugate system *xa* *xb*, where *x* is the common factor and *a* and *b* are mutually prime, may be obtained by adding 4 785 $\log_{10}x$ to the corresponding value in the system *a* *b* For values of *x* from 2 to 6 these quantities are as follows

x	2	3	4	5	6
4 785 $\log_{10}x$	1 44	2 28	2 88	3 34	3 72

In calculating the phyllotaxis index of an *x*-jugate apex from measurements taken on transverse sections, the primordia should be numbered so that *x* of them (those of the same age) receive the same number, e g in the trijugate the first nine receive respectively 1, 1, 1, 4, 4, 4, 7, 7, 7, and so on If these numbers are interpreted as ages in 'plastochrones' all the necessary adjustment in calculating phyllotaxis index will appear automatically in the determination of $\log_{10}r$ The opposite decussate system should be numbered 1, 1, 3, 3, 5, 5,

A 3 *Equivalent phyllotaxis index*

Equivalent phyllotaxis index = phyllotaxis index + 2 3925 $\log_{10}\sin\theta$, where θ is the inclination of the apical region under consideration to the axis of the shoot The angle 2θ may be determined from a longitudinal section as the inclination of two opposite sides of the apex to one another Alternatively $\tan\theta$ may be obtained from measurements on serial transverse sections (see p 540) Below are tabulated, in steps of one-tenth of a unit, the appropriate amounts to be *subtracted* from the phyllotaxis index for the various ranges of 2θ and $\tan\theta$

2θ (degrees)	$\tan\theta$	correction	2θ (degrees)	$\tan\theta$	correction
180	∞	0 0	47 3	0 437	1 0
144 7	3 147	0 1	42 7	0 391	1 1
119 9	1 729	0 2	38 6	0 350	1 2
103 7	1 272	0 3	35 0	0 315	1 3
91 1	1 020	0 4	31 7	0 283	1 4
80 9	0 852	0 5	28 7	0 256	1 5
72 2	0 729	0 6	26 0	0 231	1 6
64 7	0 633	0 7	23 6	0 209	1 7
58 1	0 556	0 8	21 4	0 189	1 8
52 4	0 492	0 9	19 4	0 171	1 9
47 3	0 437		17 6	0 155	2 0
			16 0	0 140	

A4 *Conversion table*

In order to avoid the necessity of calculating a phyllotaxis index for every apex measured the following table has been compiled From the measurements taken will be obtained either plastochrone ratio (r) or $\log_{10} r$ The table gives the range of these two quantities corresponding to each one-tenth phyllotaxis unit Thus an index of 2 3 will be assigned to any apex whose plastochrone ratio lies between 1 4127 and 1 4629, or in which $\log_{10} r$ lies between 0 1501 and 0 1652 In growth studies $\log_e r$ may be required, and this also is tabulated, intermediate values sufficiently accurate for most purposes may be obtained by interpolation

r	$\log_{10} r$	$\log_e r$	phyllotaxis index
32 47	1 5114	3 4802	
			0 0
23 59	1 3727	3 1609	
			0 1
17 65	1 2468	2 8708	
			0 2
13 56	1 1324	2 6074	
			0 3
10 68	1 0285	2 3682	
			0 4
8 592	0 9341	2 1509	
			0 5
7 053	0 8484	1 9535	
			0 6
5 896	0 7706	1 7743	
			0 7
5 010	0 6999	1 6115	
			0 8
4 322	0 6356	1 4636	
			0 9
3 778	0 5773	1 3293	
			1 0
3 345	0 5243	1 2073	
			1 1
2 994	0 4762	1 0966	
			1 2
2 707	0 4325	0 9959	
			1 3
2 471	0 3928	0 9046	
			1 4
2 274	0 3568	0 8216	
			1 5
2 109	0 3241	0 7462	
			1 6
1 969	0 2943	0 6777	
			1 7
1 851	0 2673	0 6155	
			1 8
1 7490	0 2426	0 5591	
			1 9
1 6616	0 2205	0 5078	
			2 0
1 5859	0 2003	0 4612	
			2 1
1 5202	0 1819	0 4189	
			2 2
1 4629	0 1652	0 3804	
			2 3
1 4127	0 1501	0 3455	
			2 4
1 3686	0 1363	0 3138	
			2 5
1 3298	0 1238	0 2850	
			2 6
1 2955	0 1124	0 2589	
			2 7
1 2650	0 1021	0 2351	
			2 8
1 2380	0 09274	0 2135	
			2 9
1 2140	0 08423	0 1939	
			3 0
1 1926	0 07650	0 1762	
			3 1
1 1735	0 06948	0 1600	
			3 2
1 1564	0 06311	0 1453	
			3 3
1 1411	0 05732	0 1320	
			3 4
1 1273	0 05206	0 1199	
			3 5
1 1150	0 04728	0 1089	
			3 6
1 1039	0 04294	0 09888	
			3 7
1 09396	0 03900	0 08980	
			3 8
1 08498	0 03542	0 08156	
			3 9
1 07689	0 03217	0 07408	
			4 0
1 06960	0 02922	0 06728	

r	$\log_{10} r$	$\log_e r$	phyllotaxis index
1 06960	0 02922	0 06728	
			4 1
1 06301	0 02654	0 06111	
			4 2
1 05707	0 02410	0 05550	
			4 3
1 05170	0 02189	0 05041	
			4 4
1 04685	0 01988	0 04578	
			4 5
1 04246	0 01806	0 04158	
			4 6
1 03849	0 01640	0 03777	
			4 7
1 03490	0 01490	0 03430	
			4 8
1 03164	0 01353	0 03116	
			4 9
1 02870	0 01229	0 02830	
			5 0
1 02603	0 01116	0 02570	
			5 1
1 02362	0 01014	0 02334	
			5 2
1 02143	0 009207	0 02120	
			5 3
1 01944	0 008362	0 01926	
			5 4
1 01764	0 007595	0 01749	
			5 5
1 01601	0 006898	0 01588	
			5 6
1 01453	0 006265	0 01443	
			5 7
1 01319	0 005690	0 01310	
			5 8
1 01197	0 005168	0 01190	
			5 9
1 01087	0 004694	0 01081	
			6 0
1 009865	0 004263	0 009816	
			6 1
1 008956	0 003872	0 008916	
			6 2
1 008131	0 003517	0 008098	
			6 3
1 007382	0 003194	0 007355	
			6 4
1 006702	0 002901	0 006680	
			6 5
1 006085	0 002635	0 006067	
			6 6
1 005525	0 002393	0 005510	
			6 7
1 005017	0 002174	0 005005	
			6 8
1 004556	0 001974	0 004545	
			6 9
1 004137	0 001793	0 004128	
			7 0
1 003757	0 001628	0 003750	
			7 1
1 003411	0 001479	0 003406	
			7 2
1 003098	0 001343	0 003093	
			7 3
1 002813	0 001220	0 002809	
			7 4
1 002555	0 001108	0 002551	
			7 5
1 002320	0 001006	0 002317	
			7 6
1 002107	0 0009141	0 002105	
			7 7
1 001913	0 0008302	0 001912	
			7 8
1 001738	0 0007540	0 001736	
			7 9
1 001578	0 0006848	0 001577	
			8 0
1 001433	0 0006220	0 001432	

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THE BASIC PROTEINS OF CELL NUCLEI

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(*Received* 15 *May* 1951)

[Plate 20]

Cell nuclei have been isolated from various types of tissues Evidence is presented which indicates that no appreciable loss of their major components occurs during isolation Nuclei from normal cells of a particular type possess a constant composition characteristic of that type

The basic proteins extracted from such nuclei are not homogeneous When they are of the histone type they can be separated into two parts conveniently described as a main histone and a subsidiary histone fraction respectively A subsidiary product has also been obtained from protamins

A study of the chemical composition of the main histones and the protamins has shown that some of these are unquestionably species-specific The phenomenon of cell specificity of these basic proteins has also been established in a number of instances

One case of cell specificity has also been found among the subsidiary histones The difficulty of purification has prevented the detailed examination of others

The possible physiological significance of cell specificity of the basic proteins of cell nuclei is discussed

INTRODUCTION

During the past decade the present authors have been engaged on an investigation of the chemical nature of the cell nucleus, the general results of which have, at the invitation of various institutions, been recorded elsewhere (Stedman 1944, Stedman & Stedman 1947*a*, *b*) Concurrently with this general survey of the problem, a more detailed examination of the individual components has been in progress That part dealing with the basic proteins, while it has by no means reached finality, has nevertheless now furnished results of sufficient interest to warrant description The main object of the present communication is to record these results and to discuss their implications The work, however, also constitutes a contribution to our general study of the chemical components of cell nuclei, for all the compounds examined have been prepared from isolated cell nuclei and are hence components of these cell organs Advantage has therefore been taken of the opportunity thus presented of describing the methods used for the preparation of the cell nuclei from which the basic proteins have been obtained, and to present evidence indicating the extent to which they correspond in composition with the intact nucleus in the cell

It has long been known as a result of the classical researches of Miescher (1897) and Kossel (1884) that two types of basic proteins, protamins and histones, are components of the nuclei of certain animal cells In his last review of the subject, Kossel (1928) expressed the opinion that these basic proteins do not occur in all cell nuclei, 'but only in the nuclei of certain kinds of tissue' What limitations in their distribution Kossel had in mind is not disclosed, but it must be presumed from other of his statements that he believed that they were present only in fish sperm heads and in the nuclei of avian erythrocytes and of thymocytes, for it was, in fact, only in these nuclei, or in the tissues containing them, that they had been found It has now become recognized as a result of the present authors' work in Britain and of that of Mirsky and his collaborators in America that these basic proteins are much more widespread in their occurrence They have been extracted as sulphates from nuclei (Stedman 1944) isolated from various tissues, including tumours, and in the form of nucleoproteins (Mirsky & Pollister 1942, 1943), or as components of thread-like structures which have been termed 'chromosomes' (Mirsky & Ris 1948), obtained directly from a number of tissues While this work has not embraced every known type of cell, there can be little doubt that basic proteins are components of all cell nuclei in the higher animals

During the course of this work, it was observed (Stedman & Stedman 1944) that the nuclei of the liver cells and erythrocytes of the salmon differed from the sperm heads of this species in containing histones This was contrary to expectations, for, while protamins were known to occur in the sperm heads of a number of species of fish, others, in particular the cod, contain a histone This, coupled with the fact that the two types of basic protein have never been observed to occur together in the same cell, suggested that their biological functions are identical and that consequently the chemical differences which distinguish salmine (salmon protamin) from cod histone are merely expressions in an unusually marked form of the species differences which are known to occur between homologous proteins of different species Since, moreover, there was no reason for suspecting cell specificity in the basic proteins of a given species, it was anticipated that the nuclei of the somatic cells of the salmon would all contain a protamin identical with that in the sperm heads Not only did this anticipation prove to be incorrect, but there appeared to be a difference, quite outside the limits of experimental error, between the histones isolated from the nuclei of the erythrocytes and the liver cells The presence of a histone in the nuclei of the liver cells of the salmon has been confirmed in the present investigation, but owing to the difficulties experienced in procuring specimens of salmon blood it has not been possible to reinvestigate the composition of the histone from the erythrocytes The problem has therefore been examined in other species, with the results recorded in this communication A brief, preliminary account of some of the results has been published elsewhere (Stedman & Stedman 1950*a*)

ISOLATION OF CELL NUCLEI

In order to ensure that the basic proteins used in this work were actual components of the nucleus, they were, with one exception, extracted from isolated cell nuclei No single, general method for the isolation of cell nuclei, universally applicable to all types of cells, is available. Three different procedures have therefore been used respectively for fish spermatozoa, nucleated erythrocytes and cells present in compact tissues such as thymus glands, livers and tumours

Fish sperm heads

Fish sperm heads, which appear microscopically to be naked nuclei, can sometimes be isolated by a technique which, in its main points, is identical with that originally employed by Miescher (1897) Seminal fluid, obtained by stripping the live fish, is no doubt the most favourable material to employ, but this is unfortunately difficult to procure. The mature testes must, therefore, usually suffice If these are of a large size, as with the salmon, the semi-fluid contents can be readily expressed from them The material so obtained is then suspended in five times its volume of water and the suspension stirred vigorously with a mechanical stirrer for about 15 min , after which it is strained through fine muslin It is then made just acid to litmus by the addition of dilute acetic acid and, after about 15 min , centrifuged at 3000 r p m for 15 to 20 min The sperm heads, admixed with a small amount of fibrous impurity, usually sediment readily If they fail to do so, more acetic acid must be added The supernatant fluid, which at this stage is turbid, is rejected and the sediment purified by suspending it in water, preferably acidified with dilute acetic acid to assist sedimentation, and again centrifuged This process is then repeated until the supernatant fluid is perfectly clear and the sperm heads, when examined microscopically, appear to be homogeneous It has been our practice to effect the rapid microscopic examination of the material during the preparation by the use of wet smears A drop of the suspension is mixed on a slide with a drop of a solution of methylene blue, covered with a cover-slip, and immediately examined in the microscope An illustration of such a wet smear of a finished preparation of salmon sperm heads is shown in figure 1, plate 20 Figure 2, plate 20, shows another preparation, more highly magnified, after treatment with 70 % alcohol If microscopic examination reveals the presence of impurities when no turbidity is visible in the supernatant fluid, the speed and time of centrifugation must be diminished in subsequent fractionations This may, however, result in the failure of a small proportion of the sperm heads to sediment When the fractionation is complete, the preparation is dried by suspending it with intimate mixing in about 5 vol of alcohol After standing overnight, this treatment is repeated with fresh alcohol The solid is then finally suspended in dry ether and filtered on a Buchner funnel with suction

When this method is applied to the testes of the herring, of which, owing to their small size, many are required, it is inconvenient to express the seminal fluid from them individually The testes are therefore minced coarsely in a machine and the resulting pulp suspended in water and stirred as before Fragments of the membranes are then removed by straining the mixture through a fine wire gauze, after which the procedure follows the above description The same mincing process must also be applied to testes from the salmon which are not quite mature in the sense that their contents are not fluid Contrary to the general belief, such testes obtained at the approach of the spawning season yield good specimens of sperm heads, although the fractionation process is prolonged, and the purification rendered more difficult, owing to the greater bulk of fibrous impurities which must be removed

The preparation of sperm heads from the testes of the cod presents more difficulty This is doubtless due to the more complicated structure of the testes, as compared with those of the salmon and herring, and possibly also because the maturation does not proceed uniformly throughout the numerous lobes The minute size of the sperm heads, which renders their purification by fractional centrifugation difficult, is also a contributory factor. In the preparation of sperm heads from this material, the lobes of the testes are removed from the remainder of the tissue, rejecting those which are small and obviously immature, and minced Purification is then effected by the method described above It is, however, usually impossible to remove the impurities completely by fractional centrifugation. Minute fibres, tangled together and enmeshing some of the sperm heads, sediment in the centrifuge at least as readily as the free heads. The fibres are therefore liberated, and the clumps of nuclei which they cause broken up, by suspending the material in four volumes of 4 % acetic acid and stirring the suspension vigorously with a mechanical stirrer The fluid is then again strained through fine muslin and the sperm heads sedimented in the centrifuge The subsequent process of fractional centrifugation, which is continued until the fibre is completely removed, is effected with 1 % acetic acid, each fresh suspension in this liquid being stirred before centrifugation so long as clumps of mixed sperm heads and fibre are present When the preparation is obtained free from fibre it is dried with alcohol and ether by the usual procedure

Nucleated erythrocytes

All methods for the preparation of nuclei from nucleated erythrocytes depend upon laking the washed cells and removing the haemoglobin by washing the nuclei repeatedly with physiological saline Different laking agents have been used Ackermann (1904), for example, used water The common procedure, however, is to employ saponin We have used both these methods and have also occasionally substituted cetavlon for saponin For various reasons none of the methods has proved to be uniformly successful, many of the difficulties experienced being due to the great resistance of a small proportion of the cells to the laking agent In all our experiments sodium oxalate (0 2 g /100 ml blood) has been used as anti-coagulant The oxalated blood was centrifuged and the corpuscles washed three times with physiological saline in a volume approximately equal to that of the plasma removed When water was used as a laking agent, a measured volume was added to about half its volume of corpuscles and the mixture stirred with a glass rod until it became dark in colour and clear to the unaided eye, a change which occurred in about 1 min A volume of a 1 7 % solution of sodium chloride equal to that of the water used was then added and the mixture again stirred The mixture was then centrifuged, the dark red supernatant solution rejected and the residue washed with physiological saline until it was evident from the presence of red corpuscles beneath the mass of yellow nuclei that laking had been incomplete Even after repeating this treatment several times some erythrocytes remained unlaked Meanwhile, however, changes in the nuclei had occurred In one experiment with fowls' blood, a proportion of the nuclei had coalesced together in the form of jelly-like masses In this particular case it was possible to remove these by straining a suspension of the nuclei in saline through muslin. The suspension was then centrifuged at low speed for about a minute, which caused the remaining unlaked corpuscles to collect at the bottom of the tube leaving the nuclei in a sufficiently loose state in the supernatant fluid to be pipetted from the corpuscles This experiment yielded a serviceable preparation of nuclei, but in all other and subsequent applications of this technique to fowls' blood, the nuclear material coalesced completely to a viscous mass which appeared to contain no whole nuclei whatsoever It was, moreover, contaminated with haemoglobin, which could not be removed by washing with saline. Similar results were obtained in two experiments with blood from the salmon, but with this material laking was fortunately complete, and it proved possible to remove the haemoglobin completely from the product by washing with saline This product served as the nuclear material from which histone was isolated in our earlier experiments

In most of our preparations of nuclei from erythrocytes haemolysis has been effected by saponin In a few cases, however, cetavlon has been used An identical procedure has been adopted with both haemolytic agents The washed corpuscles from fowls' blood are mixed with 2 vol of a 0 3 % solution of the haemolytic agent in physiological saline and stirred for about 2 min An equal volume of saline is then added and the mixture allowed to stand for 15 min It is then centrifuged and the residue washed several times with physiological saline A small proportion of intact erythrocytes is always present at this stage These residual cells cannot be haemolysed by short contact with the haemolytic agent It is necessary to leave them overnight (about 12 hr) with a 0·3 % solution of agent, when haemolysis is complete and the haemoglobin can be completely removed by washing the nuclei with physiological saline Even with this method, however, some jelly-like particles, presumably formed by the coalescence of some of the nuclei, are present These can be removed by straining the suspension through muslin The nuclei are then washed successively with 50 %, 70 % and absolute alcohol, the washing with the latter solvent being repeated as many times as is necessary completely to remove the yellow pigment which is usually, but not invariably, associated with fowl erythrocyte nuclei They are then suspended in ether and filtered at the pump Microscopic examination of nuclei prepared by this method reveals the fact that a proportion of the nuclei, although free from haemoglobin, retain the stroma Thus, in wet smears of the undried preparations an outline ('ghost') of the whole cell, retaining its original oval shape and containing a nucleus in the centre, can sometimes be seen, while in preparations treated with alcohol or completely dried a fine jagged protruberance, evidently consisting of part or all of the stroma, juts out from the surface of many, but not all, nuclei The proportion of nuclei retaining stroma can, we believe, be considerably diminished by vigorously stirring a suspension of the nuclei from the final saline washing in 4 % acetic acid, straining through muslin and repeating the treatment on the centrifuged material with 1 % acetic acid We have, in fact, adopted this procedure in most of our preparations One disadvantage of the use of haemolytic agents lies in the apparent ability of the nuclei to retain a small quantity of them That saponin is so retained has been shown in some unpublished determinations of furfurol-yielding substances which Dr A B Roy has carried out in his laboratory on some of the above preparations The results show that nuclei from fowl erythrocytes prepared with the aid of saponin yield considerably more furfurol than do those obtained by other means It is clear that this extra furfurol originates from saponin retained by the nuclei

The saponin method has only been used on one specimen of erythrocytes from the salmon, and this was unfortunately too small to be of further use in the present investigation. It is mentioned here, however, because of its anomalous behaviour On centrifuging the liquid after treatment of the washed cells with saponin two layers were obtained: a lower one comprising the bulk of the material and consisting of a red gel, and a small upper one of colourless liquid It appeared as if the gel had been formed by the combination of the haemoglobin with the nuclear material under the influence of the saponin On breaking up the gel with a rod, stirring it with saline and again centrifuging, the volume of the gel diminished and the saline removed some of the haemoglobin By repeating this process several times the nuclear material was obtained as a colourless jelly which yielded a white solid on drying

Compact tissues

Nuclei from compact tissues are obtained by treating the pulp with 4 % acetic acid, straining the product and fractionally centrifuging it in 1 % acetic acid according to the procedure recently described elsewhere (Stedman & Stedman 1950*b*) In applying this method to the thymus glands and spleens of the fowl, it was necessary, owing to the small size of these organs, to use material from not less than three dozen chickens in each preparation In order to avoid deterioration during the collection of this material, each gland was frozen hard in solid carbon dioxide immediately after being dissected out of the animal and maintained in this condition until used Storage in this condition was never prolonged beyond 3 days The glands from about 150 chickens were eventually required to provide sufficient material for this investigation Salmon livers, sent to us from a distance, were similarly stored in solid carbon dioxide during transit

Preparation of nuclear material from wheat germ

Owing to the presence of the cellulose cell membrane, it has not proved possible to isolate nuclei from plant material by methods similar to those used with animal tissue In order to confirm the presence of basic proteins in plant cell nuclei and to isolate such a protein for examination, nuclear material has been prepared from wheat germ by a method based on that of Mirsky & Pollister (1942)

Some non-nuclear material is first removed by suspending the wheat-germ (600 g), previously ground in a mortar, in 2 l of physiological saline and stirring the mixture for about 15 min The material is then centrifuged for 20 min at 2000 r p m The turbid supernatant liquid is discarded and the extraction process repeated on the solid After this second extraction, the solid is stirred with 1 l of 10 % sodium chloride, allowed to stand with occasional stirring for 6 hr and centrifuged at 2500 r p m for 20 min The viscous, yellow supernatant liquid is strained through muslin to remove the coarser of the particles which are still suspended in it A second extract is prepared from the solid residue in the same way and the two combined extracts are clarified in a Sharples' centrifuge This removes some small yellow particles, presumably of cytoplasmic origin, together with a finely divided, buff-coloured substance The nucleoprotein is precipitated from the clarified extract by slowly pouring into it with continuous stirring 3 vol of water The viscous nucleoprotein separates and rises to the surface as a coherent mass It can be readily removed from the slightly turbid liquid by collecting it on muslin. By way of purification, it is redissolved in 10 % sodium chloride and the solution, after clarification, reprecipitated, a process which can be repeated two or three times But with each successive precipitation the nucleoprotein becomes less coherent, and hence more difficult to collect, and finally fails to precipitate at all. It is evident from this behaviour that each precipitation is associated with a loss of protein.

EFFECT OF ISOLATION PROCEDURE ON THE CHEMICAL COMPOSITION OF CELL NUCLEI

It has been tacitly assumed in our former investigations (Stedman & Stedman 1947*b*) that the cell nuclei isolated by the acetic acid procedure mentioned above retain intact their major components Any lipids which may have been present are deliberately removed by the alcohol-ether treatment, but, apart from compounds of this type, it has been assumed that little is lost from the nucleus except, perhaps, inorganic material and, possibly, small amounts of substances of low molecular weight which do not combine with nucleic acid There were two reasons for this assumption, the isolated nuclei, when examined microscopically, appear to be identical with the corresponding nuclei in histological sections, they also react to staining procedures in much the same way Thus, as is evident from an illustration of one of our preparations of ox liver nuclei shown elsewhere (Stedman & Stedman 1950*b*), the nucleoli and 'chromatin' particles were still present and retained their capacity to take up basic dyes Secondly, analyses of numerous preparations of nuclei from a particular organ of one species gave, within narrow limits, identical results, which were, moreover, consistently different from the similarly identical results obtained from another organ Not only was this the case, but morphologically identical nuclei from several species of mammals were found to contain corresponding components in almost the same proportions Thus, the nuclei of lymphocytes obtained from the spleens of mice contained virtually the same percentage of nucleic acid and histone as did nuclei from the thymocytes of the calf and man The same correspondence obtained between the nuclei of liver cells from the ox and the mouse Taken altogether, these results constitute prima facie evidence of the validity of our assumption Pollister & Leuchtenberger (1949) have, however, pointed out that whereas our isolated nuclei contain protein and nucleic acid in a ratio of about 2, the values determined by cytological absorption measurements on various interphase and prophase nuclei range from 6 5 to 20 If we take a ratio of 10 1 as the most common value obtained by the cytological procedure, this would mean that, during the period of isolation, our nuclei had lost 80% of their content of protein or about 75% of their dry weight That nuclei could retain their characteristic structure after sustaining such a loss in their substance is, we believe, manifestly impossible But since, according to Pollister & Leuchtenberger, 'there seems [from their experiments] good reason to suppose that the more drastic procedures [for isolating cell nuclei] would reduce the protein content of nuclei' to the values of those of our preparations, we describe below experiments, carried out some years ago during the period when we were exploring methods for the isolation of cell nuclei, which show that our procedures do not, as the above authors suggest, produce any significant change in the composition of cell nuclei

The first of these experiments concerns fowl erythrocyte nuclei As pointed out above, our practice is to lake the erythroyctes with a solution of a haemolytic agent in saline This does not, as does the method used with compact tissues, necessitate the treatment of the nuclei with 4% acetic acid It nevertheless seemed desirable in order to facilitate their subsequent chemical examination to submit them to this treatment One batch of nuclei obtained by laking the corpuscles with cetavlon and removing the haemoglobin with saline was divided into two portions, one of which was dried with alcohol and ether while the other was stirred with 4 % acetic acid for 15 min and left in this solvent overnight before being so dried Unfortunately, the former (saline) preparation was dried directly with absolute alcohol without prior washing with aqueous alcohol and was consequently contaminated with sodium chloride The nucleic acid contents of, and yields of histone chloride from, the two preparations were· saline, 34 5 % nucleic acid, 25·3 % histone chloride, acid, 38 1 % nucleic acid, 28 0 % histone chloride The small differences between the results can clearly be accounted for by the contamination of the saline preparation with sodium chloride This is confirmed by the value of 37 1 % obtained for the nucleic acid content of each of two other saline preparations isolated under the same conditions except for the use of saponin as haemolytic agent and aqueous alcohol for removing the sodium chloride It is clear that treatment of nuclei with 4 % acetic acid during the isolation process does not materially affect their composition

A second experiment was made with ox liver The original purpose of this experiment was to ascertain if the purity of nuclei prepared from compact tissues could be improved by washing the tissue pulp with saline prior to its treatment with 4 % acetic acid Our final preparations of dry nuclei are, in general, almost white, but those obtained from liver usually exhibit a very faint brown tinge, probably due to the adsorption of small amounts of degradation products of haemoglobin By washing the minced tissue with saline it was hoped to avoid this contamination The finely minced liver (about 4 lb in weight) was divided into three portions 1, 2 and 3 Of these 1 and 3 were stirred vigorously for 15 min with a mechanical stirrer (not blender) with about two volumes of 0 85 % sodium chloride The mixture was then centrifuged at 2000 r p m for 20 min , the coloured supernatant fluid, which contained many small granules in suspension, rejected and the sediment again stirred, this time manually, in the centrifuge tubes with more saline After centrifuging, washing in the latter manner was twice repeated on the residue, the material thus having been subjected to a total of four extractions with saline Portion 1 was then treated with 4 % acetic acid and worked up by the customary procedure Owing to the strain on our resources of apparatus caused by the attempt to prepare three separate batches of nuclei simultaneously, it was necessary to leave portion 3 in saline for about 6 hr , otherwise, the treatment it was subjected to was identical with that described for portion 1 Portion 2 served as a control It was worked up without delay by our normal acetic acid procedure, i e without the preliminary washings with saline to which 1 and 2 were subjected The finished preparations of nuclei differed little in microscopic appearance The proportion of contaminating cytoplasmic granules was, if anything, slightly smaller in the preparations washed with saline, but it was, in any case, negligible in amount in all preparations. The dried products did, however, exhibit some difference in colour, the saline preparations being of a purer white than the other. Analyses gave the following results for the nucleic acid contents and yields of histone sulphate no 1, 30 7 % nucleic acid, 25 5 % histone sulphate, no 2, 28 7 % nucleic acid, 24 0 % histone sulphate, no 3, 30·5 % nucleic acid, 27·0 % histone sulphate. It is clear that the two saline preparations are, within the limits of experimental error, identical in composition, despite the widely different lengths of time with which the tissue from which they were prepared were in contact with the 0 85 % solution of sodium chloride The normal preparation, however, contained slightly smaller amounts of both nucleic acid and histone: these differences were certainly outside the limits of experimental error with the former and probably with the latter component. Nevertheless, the differences are small. In our opinion they are best interpreted as due to the greater freedom from contamination of the nuclei prepared with the use of saline. We have not, however, incorporated this saline procedure into our routine method for preparing cell nuclei from compact tissues because the slight increase in purity which results does not seem to justify the much greater labour which it involves.

Another experiment bearing on this theme is one which was designed to test the efficacies of different concentrations of acetic acid in cytolyzing cells. The pulp obtained by finely mincing about 2 lb. of ox liver was divided into two portions, which were treated with 4 and 1 % acetic acid respectively. On microscopic examination of the products during the process of fractional centrifugation it was observed that, while the 4 % acetic acid had effected a virtually complete liberation of the nuclei, the 1 % acid had been so ineffective in this respect that the nuclear fraction contained a large proportion of whole liver cells. Nevertheless, both preparations were brought as far as possible to completion. The 4 % acid treatment gave a normal good preparation of nuclei free from serious contamination in a yield of 2.1 g. (air-dry weight). On the other hand, the 1 % acid treatment gave a product contaminated with a small proportion of whole liver cells in a yield of 1.75 g. Analyses gave the following results: 4 % acid, 28.7 % nucleic acid, 22.5 % histone sulphate; 1 % acid, 27.0 % nucleic acid, 21.5 % histone sulphate. The difference between the yields of histone is not significant, but the smaller content of nucleic acid in the 1 % acetic acid preparation is obviously attributable to the presence in it of the visible cytoplasmic contamination. Besides demonstrating the superiority of the 4 % acid as a cytolyzing agent, the experiment also shows that it produces no more change in the composition of the nuclei than does the 1 % acid.

It is a fortunate circumstance that, while the nuclei of avian erythrocytes cannot be isolated without subjecting them to the action of saline, the nuclei from liver cells do not require this treatment but must, in the procedure which we employ, be treated with 4 % acetic acid. For this difference between the treatments required by the two types of tissue has enabled us to test in the above experiments the solvent action of 4 % acetic acid on nuclei which have been isolated in a medium of saline, and that of saline on finely minced tissue from which the nuclei can subsequently be liberated by treatment with 4 % acetic acid. It is evident from the results that, if one rejects as wholly improbable the possibility that the two liquids exert precisely identical solvent effects, neither 0.85 % sodium chloride nor 4 % acetic acid removes any appreciable amount of the major components from cell nuclei. Taken in conjunction with the other evidence recorded above this means, in our opinion, that the protein-nucleic acid ratios of the nuclei which we have prepared represent within narrow limits those which they possessed when intact in the cells from which they originated. It further means that the widely different values obtained by Pollister & Leuchtenberger are erroneous. It is, however, unnecessary to inquire in detail into the source or sources of their error, for Ris & Mirsky (1950), using, as did Pollister & Leuchtenberger, the apparatus designed by Pollister & Ris (1947), find that if they apply to their own results the methods employed by Pollister & Leuchtenberger for calculating the nucleic acid content of nuclei from measurements of their optical densities due to Feulgen staining, the results are only 25 % of those obtained by direct chemical determination. If it is true, as this suggests, that Pollister & Leuchtenberger's nucleic acid values are only one-quarter of their correct values it is obvious that, after applying the necessary correction to their results, their protein-nucleic acid ratios would come into approximate concordance with ours. A misinterpretation by Pollister & Leuchtenberger of the value of Feulgen staining for quantitative work does not, however, appear to be the sole source of error in optical measurements of this kind, for Di Stefano (1948), working in Pollister's laboratory, determined the nucleic acid content of nuclei by measurements of optical densities in ultra-violet light and obtained values which were in complete agreement with those found with Feulgen staining. From investigations of various aspects of Feulgen's reaction (Stedman & Stedman 1948, 1950*b*, Ely & Ross 1949, Ris & Mirsky 1950), it is now certain that the technique used by Pollister & Leuchtenberger cannot possibly yield correct values for the nucleic acid content of cell nuclei, and it is therefore clear from Di Stefano's result that measurements made with ultra-violet light are also subject to large error.

EXTRACTION OF BASIC PROTEINS FROM CELL NUCLEI

It has been known since the original work of Miescher (1897) on salmon sperm heads and the extension of his methods to the nuclei of avian erythrocytes by Kossel (1884) that basic proteins can be extracted from certain isolated cell nuclei or from nuclear material by means of dilute mineral acids. This method has, in fact, usually been employed for the preparation of protamins and histones from fish sperm heads and of histones from nucleated erythrocytes. Nevertheless, the histone from the thymus gland of the calf, which is the only member of this group of basic proteins which has hitherto been submitted to any extensive chemical investigation, has always been prepared by other methods (Lilienfeld 1894, Felix & Rauch 1931) from the whole gland. The basic proteins used in the present investigation have, with the exception of that from wheat germ, been extracted from isolated cell nuclei. This procedure not only ensures that they do, in fact, originate from the nucleus, but it also constitutes an important step in their purification.

Histones

For the extraction of histones, 2 g of dry cell nuclei are weighed into each 50 ml centrifuge tube used. Since dry nuclei do not easily wet with aqueous solvents, they are stirred with a small amount of absolute alcohol until thoroughly wet with this solvent. The resulting paste is treated with excess of water and, after mixing, centrifuged. The clear supernatant liquid is rejected and the solid again brought into fine suspension in water and left overnight to soak in this solvent. The water is removed by centrifugation and the solid intimately mixed with 20 ml of 0·1 N-sulphuric acid. After 20 min, during which time the mixture is frequently, although not continuously, stirred, the tube is again centrifuged and the clear, acid, supernatant liquid pipetted from the residue and treated with excess (about 40 ml) of absolute alcohol. An immediate precipitation of the sulphate of the histone usually occurs, but as complete flocculation only takes place slowly the mixture is left overnight, or longer if necessary, for this to occur. Meanwhile, the residue is again similarly extracted with 0·1 N-sulphuric acid and the process repeated until the acid extract fails to give a turbidity with excess of alcohol About eight successive extractions are normally necessary to remove the histone completely, although the bulk of the product is contained in the first three extracts The various fractions of the histone sulphate so prepared are collected together in the centrifuge and dried by two treatments with absolute alcohol and one with dry ether The suspension in ether is then filtered at the pump, when the histone sulphate is obtained as a light, snow-white powder The yield is calculated from the weight of the air-dry substance

This extraction procedure has proved to be uniformly successful when applied to nuclei prepared from compact tissues, but difficulties have sometimes, although by no means invariably, been encountered when it has been used with fowl erythrocyte nuclei In such cases treatment of the nuclei with water has caused the latter to coalesce to a sticky mass which is impenetrable to the acid added subsequently When this has occurred, it has been necessary to dry the nuclear material with alcohol, which eventually causes it to set to a hard, brittle mass, and to resume the extraction of the latter with acid after grinding it to a powder Losses of material necessarily occur during this treatment For this reason, and because histones are not so readily extracted from such material as from a fine suspension of nuclei, a low yield of histone almost certainly results The cause of this phenomenon is obscure As far as we are aware, however, it has only occurred with preparations which have not been treated with 4 % acetic acid, which reagent no doubt exerts a slight fixative or coagulative effect on the nuclear contents Such coalescence of the nuclei prepared by the saline treatment has not occurred when the material, wetted with alcohol, has been treated directly with the acid used for the extraction without first washing away the alcohol

In most of our work the histone has been prepared in the above manner in the form of its sulphate For some purposes it is convenient to prepare the chloride This can be effected by the same procedure using 0 1 N-hydrochloric acid in place of the sulphuric acid and precipitating the chloride with acetone The chloride is apparently much more soluble than the sulphate, and is not precipitated from aqueous solution by alcohol When acetone is used for this purpose, a very large excess must be added The chloride dissolves in water to give a clear, colourless solution, but if it is desired to reprecipitate it with acetone it is advisable, if the use of very large volumes of acetone is to be avoided, to add a moderate excess of hydrochloric acid to the solution The solid chloride is dried by treating it twice with acetone and once with ether It is filtered, as in the case of the sulphate, from the latter solvent at the pump

Protamins

The two protamins, clupeine and salmine, present in the sperm heads of the herring and salmon respectively, can be extracted from these nuclei in the form of sulphate by the method used for histones. Alternatively, the extraction may be made with 0 1 N-hydrochloric acid and the sulphate precipitated from the extract by the addition of sulphuric acid as well as alcohol. As pointed out elsewhere (Stedman & Stedman 1947*b*), however, decinormal mineral acid, while removing a considerable proportion of the protamin from the sperm heads, does not remove it completely in ten extractions Hence, for quantitative estimations of the amount present in the sperm heads we have employed

0 5 N-sulphuric acid, which removes the protamin so rapidly that only three extractions are found to be necessary Whichever extraction procedure is employed, the protamin sulphate usually separates on the addition of alcohol as an oil. This is allowed to settle; the mother liquor is then decanted and the oily deposit stirred with absolute alcohol, when it solidifies. It is resuspended in alcohol and finally in ether, from which it is removed by filtration

Basic proteins from nucleoproteins

Extraction of basic proteins from the nucleoprotein obtained from wheat germ has been effected with decinormal sulphuric acid in the manner described for histones Owing to the great tendency of the nucleoprotein to clot to a mass when treated with acid, some difficulty has, however, been experienced in doing this A similar difficulty has arisen in extracting histone from the nucleoprotein obtained by submitting minced calves' thymus glands to the treatment described for wheat germ Our experience with this type of material has not been extensive, but the best results seemed to be obtained by stirring the nucleoprotein with the acid, allowing the solid to settle by gravity alone and, after removing the extract, repeating the process until no further basic protein is removed The histone sulphate is then obtained from the extracts in the usual manner

BASIC PROTEIN CONTENT OF CELL NUCLEI

The yield of basic protein extracted from isolated cell nuclei by the above method is regarded as a measure of the histone content of the particular type of nucleus used It obviously does not give an absolutely accurate value for, in most cases, it is impossible to correct the yield for the weight of sulphuric acid combined with the histone Moreover, an isolation procedure can rarely be effected with quite the precision of a trustworthy method of analysis For these reasons it has seemed sufficiently accurate to calculate the percentage content of basic protein in the cell nuclei which we have examined as the weight of air-dry sulphate isolated from 100 g of air-dry nuclei Provided the extraction has been complete and losses during precipitation and manipulation have been avoided, such a method should give a somewhat high value Incomplete extraction of a sufficient magnitude materially to affect the result can, we believe, be excluded In order, however, to provide a rough check as to the possibility of other losses occurring we have, in a few cases, determined the weight of the residue from the extraction of the histone after thoroughly washing it with water and drying it with alcohol and ether This has shown that the sum of the weights of histone sulphate and residual nuclei is usually slightly smaller than the weight of the original nuclei For example, 8 g of thymocyte nuclei from the calf yielded 2·12 g (26 7 %) of histone sulphate, while the residue weighed 5 76 g (72 %) The sum of the two products thus amounted to 99 % of the weight of the nuclei taken Another preparation of similar nuclei gave 27 3 + 73·2 % = 100 5 % It follows from such results that the yield of the sulphate provides a reasonable and serviceable value for the content of histones in the cell nucleus One slight discrepancy, which we cannot yet definitely explain, has, however, recently arisen As will be seen below, when the histone is isolated in the form of chloride instead of sulphate the yield is slightly higher. That this difference is not due to a variation in the composition of the nuclei has been shown in one instance by extracting equal portions of the same batch of nuclei with sulphuric and hydrochloric acid respectively The yield of hydrochloride proved to be somewhat higher than that of the sulphate One possible explanation of this result is that the chloride which precipitates contains more equivalents of anions than does the sulphate

When determined in the above manner, the histone content of nuclei of the same type proves to be remarkably constant In a score or more determinations on preparations of nuclei from different batches of calves' thymus glands values of from 27 to 29 % have been consistently obtained, although in one experiment in which the extraction was effected with hydrochloric acid, the yield of choride was 32 % Nuclei from human thymocytes give almost identical values (Stedman & Stedman 1947*b*) Those from ox spleens, which are mainly derived from cells (small lymphocytes) which are morphologically identical with thymocytes similarly gave, in two cases, yields of 28 9 and 29 9 %, values agreeing with those previously found for lymphocytes from mice There can thus be little doubt, particularly as the nucleic acid contents also correspond closely, that the nuclei of small lymphocytes and thymocytes from these three species of mammals possess compositions which are quantitatively identical, although some of the components doubtlessly differ qualitatively among the different species

The nuclei from liver cells have not been investigated so extensively as have lymphocyte nuclei Nevertheless, it is clear that they also possess a characteristic composition which differs from that of the latter both in histone and nucleic acid content Thus, many preparations of nuclei from ox livers have given values of 23 and 28 % for histone and nucleic acid respectively Two recent values for the histone content are 22 8 and 22 6 % As pointed out on p 572, however, the value for histone may rise to 25 % and that for nucleic acid to 30 % if the liver pulp is washed with saline before the nuclei are liberated It is probable that the latter figures are the more accurate ones Liver nuclei from the mouse resemble those from the ox in composition

Preparations from fowl erythrocytes provide another example of nuclei of a given type possessing a characteristic composition Six different preparations have been examined Half of these were extracted with sulphuric acid and gave yields of histone sulphate of 24 2, 22 2 and 23·6 % The remainder were extracted with hydrochloric acid and yielded 28 0, 25 3 and 29 7 % of histone chloride The low value of 25·3 % for the chloride given by one preparation was due, as explained on p 572, to the contamination of the nuclei with sodium chloride In view of the discrepancy between the yields of sulphate and chloride, separate portions of another preparation of these nuclei were extracted with the two acids They gave yields of 22 5 and 28 5 % for the sulphate and chloride respectively From phosphorus determinations on four preparations of erythrocyte nuclei, the nucleic acid contents were calculated to be 37 1, 37 1, 38 1 and 37 8 % Fowl erythrocyte nuclei thus resemble mammalian liver nuclei with respect to their content of histone and lymphocytes with respect to that of nucleic acid

A knowledge of the basic protein content of cell nuclei is important not only because its value is usually constant for, and characteristic of, normal cells of a particular type, but also because it enables an estimate to be made of the extent to which other proteins enter into the composition of various cell nuclei For this purpose it is also necessary to know the nucleic acid content, a fairly accurate value for which can be calculated from a phosphorus determination on the lipid-free, dry nuclei. It was, in fact, by this method, combined with the demonstration of the presence in nuclei of the protein chromosomin, that we were able to show (Stedman & Stedman 1943) that cell nuclei, which had formerly been thought to be composed entirely of histone (or protamin) nucleate (see Stedman & Stedman 1947*a*) were, in fact, more complex and contained three main components nucleic acid, basic protein and chromosomin. As pointed out by Schmitt (1944) at the time, this result was in direct conflict with the work of Mirsky & Pollister (1942, 1943), who adhered to the classical view of the composition of cell nuclei. Mirsky & Pollister (1947) and Mirsky & Ris (1948) have, however, since confirmed the presence of chromosomin in cell nuclei. Nevertheless, they still maintain that the nuclei of calf thymocytes contain over 90 % of histone nucleate. This conclusion is in such direct conflict with our results that it is necessary to consider the basis of their claim.

In their more recent work, Mirsky & Ris (1948) use material which they describe as 'chromosomes'. We do not share their view of the nature of this material. It contains, it is true, threadlike structures, but these are unlike any known chromosomes. Moreover, according to Calvet, Siegel & Stern (1948), who have made an electron microscopic study of the so-called chromosomes, they consist of 'random fragments of the chromatin network'. Lamb (1949), in similar studies, concludes that they are formed by drawing out the nuclei into thread-like formations which later break off as isolated threads. There is, however, evidence of an even more convincing nature that the thread-like structures are not chromosomes, they possess a composition which is to all intents and purposes identical with that of the intact nucleus from which they originated. This follows, in the case of thymocyte 'chromosomes', from their nucleic acid content. Thus, Mirsky & Ris (1948) state that their lipid-free 'chromosomes' from calf lymphocytes contain 37 % of their weight of nucleic acid. According to Stedman & Stedman (1947*b*) the lipid-free nuclei also contain 37 % of nucleic acid. Similarly, Mirsky & Pollister (1947) converted isolated thymocyte nuclei into nucleoprotein by dissolving them in molar saline and precipitating the nucleoprotein by dilution with water. This material again contained 37 % of nucleic acid. These results lead inescapably to the view that the 'chromosomes' are identical in composition with the nucleus itself. Ris & Mirsky (1949) have, indeed, been forced to the conclusion that their 'chromosomes' do, in fact, fill the whole nucleus, a conclusion which, in our view, constitutes a *reductio ad absurdum*. Evidently Mirsky & Ris's threads are not chromosomes. If they were, a dilemma would arise of the same nature as that caused by the classical view of the composition of cell nuclei, the resolution of which has been outlined elsewhere (Stedman & Stedman 1947*a*), this solution still holds.

Mirsky & Ris claim that their 'chromosomes', which, as we have seen, are identical in composition with the whole nucleus, contain 55 % of histone. With a nucleic acid content of 37 %, the nucleohistone content thus becomes 92 %. On the other hand, on the basis of our results the nucleohistone content should not exceed 70 %. There is obviously a big discrepancy between the two results. Mirsky & Ris suggest that this is due to the impossibility of extracting histone completely from isolated nuclei, a view which will be considered below. In our opinion, much of the discrepancy is due to the methods used by these authors both for measuring and for calculating the histone content of their 'chromosomes'. To do this they dissolve them in molar saline and centrifuge the solution at high speed. This causes some chromosomin, contaminated or combined with a small proportion of nucleic acid, to sediment, but there is no evidence that its sedimentation is complete. They then ascertain the nucleic acid content of the nucleoprotein contained in the supernatant by precipitating it from an aliquot of the fluid and determining the phosphorus content of the dry material. The value obtained is 45 %. Histone determined in another aliquot colorimetrically is said to constitute 47 % of the mass of the fibrous nucleoprotein in the supernatant. The sum of the two components amounts to 92 %, and Mirsky & Ris therefore conclude that 8 % of the histone has been lost in the determination. If this is added to the 47 % estimated, a total of 55 % is obtained which, when added to the 37 % of nucleic acid originally present in the 'chromosomes', gives a total of 92 % of histone nucleate in the latter. It is, of course, clear that this figure is arrived at, not as a result of the estimation of histone, but largely on the basis of the weight (8 %) of chromosomin in the sediment produced by the centrifugation of the solution in molar saline. There is, moreover, an error in Mirsky & Ris's calculations. A value of 47 % histone in the material containing 45 % nucleic acid corresponds with a value for histone of 38 % in the original 'chromosomes', which contained only 37 % nucleic acid. The sum of the histone and nucleic acid contents of the original material thus becomes 38+37=75 %, a figure which approximates to the 70 % maximum of our results. It should be noted that the Millon colour which Mirsky & Ris reported to be present on the precipitate which formed during the above estimation of histone, and which they attributed to histone, could well be due to chromosomin which had escaped sedimentation during centrifugation.

In view of the conflicting results yielded by our methods and those of Mirsky and his collaborators on the composition of the nuclei of calf thymocytes, it is of interest to note that something approaching agreement has been obtained with the nuclei from ox-liver cells. According to our results, and selecting maximum figures, these contain 25 % of histone and 30 % of nucleic acid, so that the amount of histone nucleate which it should be possible to obtain from them by Mirsky's method is 55 %. According to Mirsky & Ris 'chromosomes' from calf livers contain 45 % of histone nucleate. Evidently our method of extraction has, in this case, given quantitative yields of histone. There is thus no reason why it should not also do so, as we are confident it has done, with the nuclei from thymocytes.

As pointed out above, Mirsky & Ris consider that it is impossible to extract histones quantitatively from cell nuclei. There is a considerable discussion on this subject in the older literature culminating in the failure of Steudel & Peiser (1922) to extract histone quantitatively by means of dilute mineral acid from histone nucleate prepared from the two components, and hence known to contain only these components. The explanation of this failure is simple and of a purely physical nature. The nucleic acid, liberated by the mineral acid from its combination with histone, immediately forms a sticky mass through which the solvent is unable to diffuse. Hence complete extraction of the histone is impossible. Cell nuclei do not, however, consist solely of histone or protamin nucleate, although this view obtained at the time Steudel made his experiments. They also contain chromosomin, and there is little doubt that the difficulties experienced in extracting histone or protamin from the nucleates of these bases are minimized in cell nuclei because the nucleic acid, liberated from its combination with the base, then combines with chromosomin Nevertheless, as the experiments described above show, difficulty is sometimes encountered with cell nuclei, but this has only occurred with nuclei which have not been submitted to the 4 % acetic acid treatment. With such nuclei the extraction of histone proceeds smoothly and without difficulty

PURIFICATION OF HISTONE AND PROTAMIN SULPHATES

Histones

The sulphates of the histones prepared by the above method from various cell nuclei were, in our earlier experiments, purified by dissolving them two or three times in water acidified with a small amount of dilute sulphuric acid, centrifuging the material to remove any insoluble material and then reprecipitating the histone sulphate with alcohol Table 1 gives some analyses, which are useful for comparison with later figures, made on histones from various sources purified in this way The results at first suggested that the histones present in the thymocytes, lymphocytes and liver cells of the ox were, in fact, different substances But when the tyrosine contents of numerous preparations of thymus histone sulphate from the calf were determined, discordant figures were obtained The tyrosine contents, expressed as a percentage of the dry weight of the sulphate, varied from 3 5 to 4 0 % It seemed clear from these results that a partial fractionation was being effected by reprecipitation, which had been carried out solely with a view to removing traces of insoluble material, and that this fractionation had proceeded to different degrees in the various preparations One specimen of thymus histone sulphate was therefore separated into three fractions by precipitating it from aqueous solution by the successive addition of suitable volumes of alcohol Some difficulty was experienced in doing this, for when a solution of histone sulphate is treated with an amount of alcohol insufficient to cause almost complete precipitation, the fraction which separates retains much water and consequently forms a light, jelly-like precipitate which is difficult to separate from the liquid by centrifugation The three fractions which were eventually obtained were dried with alcohol and ether and analysed for their contents of arginine and nitrogen. Two of them were also analysed for tyrosine The results are given in table 2 These left no doubt that the histone was not homogeneous The following method of purification, based on its fractional precipitation with alcohol, was therefore devised.

TABLE 1 ANALYSES OF SOME HISTONES BEFORE FRACTIONATION

species	source	salt used	N-content (%)	amide-N (% of total N)	arginine-N (% of total N)
ox	thymus	sulphate	16 1	4 69	26 1
ox	spleen	sulphate	16 3	5 00	28 8
ox	liver	sulphate	16 7	5 11	30 8
fowl	blood	sulphate	15 6	4 68	28 6
fowl	blood	chloride	17 1	5 77	28 6

Each gram of crude histone sulphate, as isolated directly from cell nuclei, is placed in a centrifuge tube and dissolved in about 40 ml. of water by rubbing it with a glass rod in the tube, a process which frequently takes about an hour owing to the sticky mass which the histone forms on being first wetted with water This solution is then centrifuged and the clear, colourless supernatant liquid pipetted from a small sediment of insoluble material into a flask. The centrifuge tube and the sediment which it contains are washed with about 15 ml of water, the tube again centrifuged and the washings united with the main solution To this is added, first, one drop of bench dilute sulphuric acid and then, slowly and with constant shaking, absolute alcohol until the solution becomes markedly opalescent Further small additions of alcohol are then made at short intervals until a slight but perceptible precipitate forms The solution is left overnight, during which time the histone sulphate settles as a bulky mass The contents of the flask are transferred to centrifuge tubes with as little disturbance as possible and centrifuged If the mixture has been shaken too vigorously during transference, centrifugation sometimes presents difficulties Otherwise, the precipitate collects as a bulky, opalescent jelly-like mass at the bottom of the tubes with a clear solution above The latter is removed with a pipette and the jelly intimately mixed with absolute alcohol, this causes a considerable contraction of the material, no doubt due to the removal of water After about an hour the tube is centrifuged, the supernatant liquid removed and the sediment again stirred with absolute alcohol Dehydration is allowed to proceed for some hours, usually overnight, when the alcohol is removed by centrifugation and the pasty residual sediment stirred with dry ether This transforms the sediment into a light, flocculent solid which is filtered with suction and carefully washed with dry ether The whole operation is then repeated three more times on the solid This procedure has been applied successfully to the crude histone sulphates isolated from cod sperm heads and the nuclei from calves' thymus glands, ox livers, ox spleens, fowl erythrocytes, fowl thymus glands, fowl spleens, salmon livers and human glands, spleen and tumour. The yields of the main products at each stage of the fractionation and the percentage yield of the final preparation are recorded in table 3 The figures are of interest in several respects The loss of weight is so much greater at the first than at subsequent precipitations that it can be assumed that the fractionation is almost completed during the first two stages Different preparations of crude histone obtained from nuclei of the same type give similar yields of the purified substance, thus demonstrating the uniformity of the fractionation process and suggesting that the impurity removed is a constant component of the nuclei and not an adventitious impurity In general, this yield is also fairly constant for different types of nuclei from the same or different species, although there is one important exception The crude histone isolated from fowl erythrocyte nuclei gave a yield of the purified histone which is definitely smaller than those from lymphocytes and thymocytes of the same species, a result which corresponds with the presence, as described on a later page, of a histone in the mother liquors from the erythrocyte histone which is absent from those of the lymphocyte and

TABLE 2 FRACTIONATION OF CRUDE THYMUS HISTONE SULPHATE FROM THE CALF

fraction	total-N (%)	amide-N (% of total N)	arginine-N (% of total N)	tyrosine (%)
most soluble	15 96	4 14	18 3	1 78
middle	17 00	5 13	28 7	4 26
least soluble	17 00	4 96	30 3	—

thymocyte histones. The slight difference between the yields from calf thymocyte and ox-liver nuclei is probably not significant, but it is mentioned here because it nevertheless conforms, as a comparison of the results in tables 1 and 4 will show, with the greater change produced by fractionation in the composition of thymus than of liver histone.

TABLE 3. YIELDS OF MAIN FRACTION OF HISTONE SULPHATE DURING FRACTIONATION

species	source	weight of crude histone sulphate (g.)	yield (g.) from fractionation no. 1	2	3	4	final yield (%)
ox	thymus	4	3.31	3.18	2.94	2.84	71
ox	thymus	4	3.30	3.15	—	2.79	69
ox	thymus	4	3.22	2.98	2.83	2.77	69
ox	thymus	4	3.27	3.02	2.86	2.71	68
ox	thymus	2.93	2.56	2.31	2.17	2.12	72
ox	spleen	1.99	—	1.42	1.38	1.28	64
ox	spleen	1.96	1.64	1.54	1.45	1.42	72
ox	liver	4	3.50	3.28	3.12	3.09	77
ox	liver	4	3.38	3.27	3.10	3.04	76
fowl	blood	2.09	1.32	1.13	—	0.99	47
fowl	blood	4	2.65	2.31	—	2.00	50
fowl	thymus	1.89	1.61	1.52	1.50	1.45	77
fowl	spleen	1.15	0.97	0.90	0.88	0.86	75
cod	sperm	1.90	1.59	1.50	1.36	1.33	70
cod	sperm	3.33	2.81	2.53	2.32	2.29	69
salmon	liver	1.45	1.25	1.15	1.07	1.03	71
man	spleen	2.00	1.67	1.60	1.54	1.46	73
man	lymph glands	2.08	1.78	1.63	1.55	1.51	73
man	broncogenic carcinoma	0.76	0.64	0.60	—	0.47	62
wheat	germ	2.00	1.50	1.34	1.21	1.09	54

The histones purified in the above manner will be referred to as the main histones of the cell nuclei from which they originate. This will distinguish them from the more soluble basic proteins, which will be provisionally termed subsidiary histones, remaining in the mother liquors.

Protamins

The two protamins, clupeine and salmine, which have been examined are so similar in properties that identical methods have been used for their purification. Thus, 1 g. of crude clupeine sulphate was dissolved in 20 ml. of water, the solution centrifuged to remove a small amount of insoluble material and the supernatant liquid treated with 5 ml. of alcohol. The colourless, oily precipitate which formed was centrifuged down and immediately stirred with alcohol, which caused it to solidify rapidly to a hard, white solid. This was then submitted twice more to the same treatment, when about 0.8 g. of the final product, known as 11V*b*1, was obtained. After the first precipitation, the product, presumably as a result of the loss of sulphate radicals, diminished in solubility, thus necessitating the use of larger volumes of water to effect solution. For reprecipitation, 5 ml. of alcohol per 20 ml. of solution was consistently used.

For comparison with the above product, 1 g. of the same crude preparation was dissolved in water and reprecipitated once only. The yield of product, which was termed V*a*, was 0.96 g.

Salmine sulphate was reprecipitated four times in a similar manner, the final preparation being known as 111X1.

METHODS OF ANALYSIS

General

The analytical procedures described in this section were carried out on material dried to constant weight in a high vacuum over phosphorus pentoxide at room temperature. Nitrogen was determined by micro-Kjeldahl and phosphorus by the method described elsewhere (Stedman and Stedman 1950*b*).

Arginine

The method employed for the estimation of arginine in proteins has been used in this laboratory since 1943. Meanwhile its essential features have been described by Macpherson (1946), although details of its application in the two laboratories differ. The method is based on the observation of Plimmer & Rosedale (1925) that, with certain reservations as to the existence of other possible sources of ammonia, arginine can be determined in protein hydrolysates by measuring the ammonia produced by their alkaline hydrolysis. Plimmer & Rosedale worked on a macro scale. We, like Macpherson, have adapted the process to a micro method. The apparatus for the alkaline hydrolysis is exceedingly simple and can be readily constructed from an ordinary micro-Kjeldahl apparatus by interposing a small reflux condenser between the head of the Kjeldahl flask and its normal condenser. The hydrolysis is then effected in the flask with the whole apparatus assembled as for a normal Kjeldahl estimation. When hydrolysis is complete, the water is run out of the reflux condenser and the ammonia blown over with steam in the customary manner. The details of its application to histones are as follows.

The histone sulphate (about 220 mg.) or protamin sulphate (about 150 mg.) is hydrolyzed by refluxing it with 7 ml. of 7N-hydrochloric acid for 30 hr. Without removing the acid, the hydrolysate is made up to 25 ml. with water, and 1, 10 and 5 ml. (2 ml. in the case of protamins) aliquots of this solution are used respectively for the determination of total nitrogen, 'amide' nitrogen and arginine nitrogen. With the exception of the 'amide' nitrogen, these are made in duplicate.

'Amide' nitrogen is determined in the ordinary micro-Kjeldahl apparatus. To the 10 ml. of hydrolysate contained in the flask is added 1 g. of calcium hydroxide made into a paste with a little water. Steam is then passed through the apparatus in the usual way.

For the arginine nitrogen, 5 ml. of the hydrolysate (or 2 ml. hydrolysate plus 3 ml. water) are placed in the flask of the modified Kjeldahl apparatus and 8 ml. of 50 % sodium hydroxide, followed by 3 ml. of water, added. The mixture is then boiled under reflux for 6 hr., when the ammonia formed is collected by steam distillation. This ammonia represents 50 % of the arginine nitrogen plus the amide nitrogen. The total arginine nitrogen is therefore twice the difference between these two values.

In testing the hydrolysis procedure with a good specimen of arginine mono-hydrochloride, the following results were obtained: total N, 25.8, arginine-N, 25.2, the theoretical nitrogen content being 26.6 %. The specimen thus contained 97.0 or 94.7 % of arginine hydrochloride according to the respective determinations with the Kjeldahl or hydrolysis procedures. If the impurity indicated by the total nitrogen content to be present in the arginine was non-nitrogenous, it is evident that, as Macpherson claims, the recovery of arginine by the hydrolysis procedure, which in the above experiment amounts to 97·7 %, is not complete. Estimations made on proteins would, in fact, require correcting by the addition of 2·3 % to the determined values. We are, however, loth to apply such a correction for the following reasons. Determination of the arginine content of salmine gave an uncorrected value, expressed as the percentage of the total nitrogen due to arginine, of 88·9. If this were increased by 2·3 %, it would become practically 91, a value which is, we believe, higher than any recorded value. Thus, recent values from the literature are 90·2 (Block & Bolling 1945*b*), 86·5 (Macpherson 1946) and 89 (Tristam 1947). While this result gives some support to the view that the impurity in our specimen of arginine is nitrogenous it is by no means conclusive. There is, moreover, a further complication due to the possibility that amino-acids other than arginine may contribute a small quota of ammonia during the hydrolysis. We have therefore deemed it preferable to quote uncorrected results. As those obtained with salmine show, these must give substantially, if not absolutely, correct values for arginine, and we have been less concerned in this investigation with absolute values for particular amino-acids than with a method of estimation which can be carried out with precision, will yield reproducible results and will therefore serve admirably for the characterization and comparison of histones from different sources. The method which we have described meets these requirements.

Tyrosine

This was determined colorimetrically with the aid of the Millon reaction, using a procedure which, in the main, follows that described by Block & Bolling (1945*a*). The exact details are as follows. The histone sulphate (about 6 mg.) contained in a small flask with a 10 ml. graduation mark on the neck is dissolved in 0·4 ml. of water, a process which is conveniently allowed to complete itself overnight. This treatment has the double object of ensuring the dissolution of the histone, which otherwise causes difficulty, and of compensating for the evaporation of water during the subsequent hydrolysis. To this solution is added 0·5 ml. of 6 N-sodium hydroxide, when the mixture is heated on a boiling water-bath without any arrangement, apart from the short neck of the flask, for preventing evaporation. After 5 hr. the flask is cooled and its contents acidified with 0·7 ml. of 7 N-sulphuric acid. Two ml. of 15 % mercuric sulphate in 5 N-sulphuric acid are then added, when the flask is heated for 10 min. on a boiling water bath. After cooling, 1 ml. of 7 N-sulphuric acid, 2 ml. of 0·2 % sodium nitrite and water to the 10 ml. mark of the flask are then added, and the optical density of the solution measured exactly ten minutes later in a Spekker absorptiometer using a spectrum blue filter. The amount of tyrosine present is read from a calibration curve, which is checked for each determination by means of a standard containing approximately the same amount of tyrosine as the unknown. No correction has been made for the destruction of tyrosine during the hydrolysis.

ANALYSES OF MAIN HISTONES AND PROTAMINS

Histones

The analytical results given by the main histone sulphates from various species and organs are given in table 4. Where complete duplicate analyses are recorded, they have been made on histones prepared from entirely different batches of cell nuclei. This has been done in as many cases as practicable. With the exception of the 'amide' nitrogen, for which only one determination has been carried out, all estimations have been made at least in duplicate. Individual figures have, however, only been quoted when replicate figures did not agree exactly.

TABLE 4. ANALYSES OF SULPHATES OF MAIN HISTONES

species	source	N content (%)	amide-N (% of total N)	arginine-N (% of total N)	tyrosine (%)
ox	thymus	17.0	4.95	29.8	4.37, 4.42
ox	thymus	17.0	5.19	29.1	4.32, 4.40 4.29, 4.32
ox	spleen	17.6	4.77	29.3	4.33, 4.25
ox	spleen	17.0	5.00	29.7	4.31, 4.41 4.35, 4.36
ox	liver	16.8, 16.7	4.99	30.4	4.32, 4.46
ox	liver	17.3, 17.2	4.93	29.5	4.45, 4.58, 4.47
fowl	blood	17.1	5.35	26.0	4.41, 4.43
fowl	blood	16.5	5.24	26.9, 26.5	4.32, 4.44
fowl	spleen	16.5	5.28	29.8	3.92, 4.34
fowl	thymus	16.6	5.07	29.4, 29.2	4.32, 4.30
cod	sperm	16.8	4.83	28.5, 28.8	3.31, 3.21
salmon	liver	16.9, 16.8	4.94	30.2	4.48, 4.51
man	broncogenic carcinoma	16.8	4.93	29.2, 29.8	4.41, 4.36
man	lymph glands	16.7	5.10	28.5, 29.3	4.60, 4.44
man	spleen	16.7, 16.9	4.74	30.6	4.38, 4.38
wheat	germ	15.1	4.23	19.5, 20.5	2.92, 2.90

In considering the bearing of the figures in table 4 on the question of the specificity of histones, two types of this phenomenon must be distinguished: species specificity and cell specificity. The former, when applied to homologous proteins, is a general phenomenon. It is exemplified in connexion with the basic proteins of cell nuclei by the protamins, salmine and clupeine, present respectively in the sperm heads of the salmon and herring, and the histone present in the sperm heads of the cod. These three proteins are clearly homologous proteins for they occur in the nuclei of similar cells and must therefore possess identical functions. The two protamins resemble one another closely in composition and were, in fact, at one time, thought to be identical. It is, however, now certain, as will be shown on p. 592, that they possess different compositions despite the small differences between the analytical results recorded in table 5. That the homologous histone of cod sperm is a different protein from the protamins has, owing to its marked difference in chemical and physical properties, never been in doubt. Species specificity of the basic proteins of cell nuclei is thus demonstrable in the sperm heads of these fishes, and there can be little doubt that it extends to the histones of other cell nuclei. Nevertheless, if the analyses for homologous histones in table 4 are compared, it is evident that they give no indication of species specificity in this sense. As far as the analyses have extended, it is impossible to distinguish between the histones from ox and salmon livers or between those from lymphocytes (or thymocytes) from the ox, fowl and man. It would be similarly impossible to distinguish between salmon and herring protamins on the basis of the small differences in their arginine contents given in table 5 were it not that other differences in their composition are present. It is thus clear that, except in favourable cases, species specificity in the basic proteins of cell nuclei is difficult to detect by purely chemical means, although it must be assumed to exist

The demonstration of cell specificity in basic proteins would, *a priori*, be expected to present more difficulties In fact, its detection seems to depend, as does that of species specificity, on the choice of favourable material When a protamin is present in the sperm head, as it is in the salmon, its difference from the histones present in the nuclei of the somatic cells is so obvious that it provides a clear-cut case of cell specificity which is as definite as that of the species specificity shown by a comparison of the basic proteins in salmon and cod sperm heads On the other hand, as a reference to table 4 will show, there is little, if any, difference between the analytical results yielded by the histones from different cell nuclei of the ox The same analytical methods, however, if applied alone, would scarcely serve to detect species specificity in salmon and herring protamins Hence the results with histones from the ox must not be taken to disprove the existence of cell specificity in this species, they must be regarded as negative The histones from the fowl present a much more favourable case Those from the spleens and thymus glands, assuming them to originate from the nuclei of identical cells, would be expected to be the same, as in fact the analyses indicate, but do not prove, that they are But the histone from the erythrocytes is definitely different in composition Its arginine content is smaller than that of the lymphocyte histone The difference, although not very large, is certainly outside the limits of experimental error The result is, moreover, supported by the fact that in the purification of the total histone isolated from fowl erythrocyte nuclei, which has an arginine content (table 1) identical with that of purified fowl thymus histone, a subsidiary histone with a higher arginine content (table 7) is removed from it Incidentally, this subsidiary histone is absent from thymocyte and lymphocyte nuclei and hence represents another example of cell specificity among the histones Cell specificity of the basic proteins of cell nuclei has thus been demonstrated to occur between the sperm and somatic cells in the salmon, and between the erythrocytes and the lymphocytes in the fowl It also almost certainly exists, as pointed out in the introduction, between the erythrocytes and the liver cells of the salmon It is thus probable that it is a general phenomenon

Protamins

Analyses of salmine and clupeine sulphates, before and after fractionation, are shown in table 5 It is clear that fractionation produces a slight change in composition Its magnitude is, however, so small that it is evident that the basic material originally isolated from the sperm heads consisted to a preponderating extent of protamin This is illustrated in a marked manner in the case of clupeine The preparation V*a* was obtained in a yield of 96 % by fractionation of the unpurified product Despite this high yield, two additional fractionations, giving preparation 11 V*b* 1, produced no further change in composition Nevertheless, as will be described on p 588, the mother liquors from the purification of both clupeine and salmine yielded a small amount of protein of a different character from the protamin

The demonstration that the unpurified protamin consisted essentially of one substance of high arginine content is of interest because, while the homogeneity of salmine has, as far as we are aware, never been questioned, this is not the case with clupeine. Following the work of Kossel (1928), it has been generally accepted that clupeine is a mixture of protamins with varying arginine contents. Our results do not support this view. The discrepancy is probably due to the use by Kossel of impure sperm heads, and possibly also to his use of hot solutions in the purification of his product, with the consequent contamination of the protamin with non-nuclear proteins and with its own partial decomposition products.

TABLE 5. ANALYSES OF SULPHATES OF PROTAMINS

species	preparation	N content (%)	amide-N (% of total N)	arginine-N (% of total N)
salmon	unpurified	22.9	0.96	87.7
salmon	111X1	24.1	0.69	88.9
herring	unpurified	22.9	0.82	86.2
herring	V*a*	24.2	0.78	87.6
herring	11V*b*1	24.1	0.65	87.9

SUBSIDIARY HISTONES

Evidence for the existence of subsidiary histones

The addition of small volumes of alcohol to the clear, colourless mother liquors obtained during the purification of the sulphates of the main histones produces no change in their appearance, but if a large excess of alcohol is added the liquid becomes intensely opalescent and, on standing, slowly deposits a white solid, a process which can usually be much accelerated by vigorously swirling the opalescent solution in the flask. When, as judged by the disappearance of the opalescence, precipitation is complete, the suspension is centrifuged and the sediment dried with alcohol and ether in the usual way. The product, while not deliquescent in the ordinary meaning of the term, tends to take up moisture from the air and to become sticky during filtration at the pump, although this can be prevented if due care is exercised. It is also much more readily soluble in water than is the main histone. Its properties thus clearly differ from those of the latter. Nevertheless, it is by no means a pure substance and is almost certainly contaminated with the main histone. In an attempt to remove this, the material so obtained was dissolved in water, the solution acidified with a drop of dilute sulphuric acid and then treated drop by drop with alcohol until a faint but permanent turbidity was produced. After a time a flocculent solid usually separated, although occasionally the liquid set to a gel. In the latter case the process was repeated with a more dilute solution, when a precipitate formed normally. The precipitate was removed in the centrifuge and the liquid treated with an excess of alcohol. This precipitated the bulk of the material, which was collected and dried by the

TABLE 6. ANALYSES OF PARTLY PURIFIED SUBSIDIARY HISTONES

species	source	N content (%)	amide-N (% of total N)	arginine-N (% of total N)	tyrosine (%)
ox	thymus	15.8, 16.0	3.38	11.5	1.40
ox	spleen	15.7	3.09	13.3	1.29
ox	liver	15.9	3.27	13.8	1.70
fowl	thymus	15.2	3.36	20.3	1.48
cod	sperm	15.2	3.20	17.3	0.81, 0.86
wheat	germ	15.2	3.00	16.2	2.54

usual procedure The analyses of such products, recorded in table 6, provides evidence, as a comparison with table 4 will show, that the mother liquors from the purification of the main histones contained one or more proteins which differ markedly in composition from them Similar products were obtained during the fractionation of the histones from human tissues, fowls' spleens and salmon livers, but the amount of material available in these cases was too small to warrant further examination On the other hand, the total histones from calves' thymocytes and fowls' erythrocytes are more readily accessible. They have therefore provided material for a somewhat more detailed examination of the nature of the products obtained in the manner described above The results, taken in conjunction with the analyses in table 6, seem to leave no doubt that the proteins associated with the main histones in acid extracts of isolated cell nuclei are basic proteins and can therefore be regarded as subsidiary histones

It is probable, although not yet certain, that a protein of the nature of a subsidiary histone is associated with the protamins present in fish sperm heads Thus, when treated with an excess of alcohol, the mother liquors from the fractionation of 2 g of salmine sulphate yielded a small amount of precipitate This was dissolved in 20 ml of water and treated with 4 ml of alcohol An oily precipitate, presumably consisting of protamin sulphate, separated This was centrifuged down and rejected Addition of excess of alcohol to the supernatant then gave a precipitate which, on drying, weighed 100 mg This, known as X 2, was used for chromatographic analysis, as will be described on a later page A similar fraction was obtained from the mother liquors from the fractionation of clupeine The amounts of these substances obtained was, however, too small for further examination

Fractionation of the subsidiary histones from fowls' erythrocytes

Corresponding with the smaller yield of main histone from the total histones extracted from the nuclei of fowls' erythrocytes (see table 3), a larger yield of subsidiary histone is obtained from this than from similar material from other tissues and species Thus, in one experiment, 2 09 g of total histone sulphate yielded on fractionation 0 85 g of crude subsidiary histones The fractionation of this material, which was termed 2F2, is best described by the use of our serial numbers 2F2 was dissolved in water, one drop of dilute sulphuric acid was then added, as in all subsequent fractionations of this material, and the solution treated with sufficient alcohol to produce an opalescence but no immediate precipitate On standing overnight, a considerable precipitate formed This was centrifuged yielding a solid 12F2 The supernatant liquid was treated with more alcohol, which caused a further precipitate 22F2 (0 28 g) to form Without drying, 12F2 was dissolved in water and alcohol added drop by drop until the solution was slightly turbid The precipitate, 112F2, which formed was removed and more alcohol added to the mother liquor giving the precipitate 212F2 (0 21 g) Again without drying, 112F2 was dissolved in water and the solution carefully treated with alcohol until just turbid, the slight precipitate which ultimately formed being rejected The mother liquor gave on the addition of alcohol 2112F2 (0 24 g) The three fractions thus obtained accounted for nearly 86 % of the original material They were analyzed with the results given in table 7.

While it is probable that none of these fractions was pure, a comparison of the results obtained with fractions 212F2 and 2112F2 indicates that the latter was approaching purity. Unfortunately, through an accident, its tyrosine content was not determined exactly, but it was roughly estimated to be of the same order as that of 212F2. In any case, it is clear from the results that one of the subsidiary histones in the nuclei of fowl erythrocytes contains a greater proportion of arginine than does the main histone. Corresponding with this finding, and therefore confirming it, the total, unfractionated histone itself contains more arginine than does the purified, main histone, as a comparison of the results in tables 1 and 4 will show. The high arginine content of this basic protein and its nuclear origin justify its designation as a histone. Since, moreover, material with a similar high arginine content was absent from the subsidiary histone fraction from the thymocytes of the fowl, the presence of this histone in fowl erythrocyte nuclei represents a marked difference in chemical composition between two types of nuclei from the same species. The fraction 22F2, which represents the most soluble fraction of the subsidiary histones from fowl erythrocytes, contains less arginine and less tyrosine than either the subsidiary histone 2112F2 described above or the main histone (table 4). We regard this as evidence of the presence in fowl erythrocyte nuclei of at least one other subsidiary histone differing from the one described above in containing a lower arginine content than the main histone.

TABLE 7. ANALYSES OF FRACTIONS OF SUBSIDIARY HISTONES FROM THE FOWL

serial no.	N content (%)	amide-N (% of total N)	arginine-N (% of total N)	tyrosine (%)
22F2	15·6, 15·7	2·93	16·93	1·10
212F2	17·2	3·48	32·1	2·60
2112F2	17·5, 17·4	3·48	34·0	

Fractionation of the subsidiary histones from calves' thymocytes

The crude subsidiary histones, weighing 3·2 g., which were available for this fractionation were obtained at various times from about 20 g. of total histone sulphate isolated from nearly 70 g. of dry nuclei from calves' thymocytes. The material, known as 2R2, was dissolved in about 60 ml. of water and the solution acidified with dilute sulphuric acid, a procedure which has been carried out at each stage of the fractionation. Attempts to precipitate from this solution a small fraction of the material by the careful addition of alcohol were unsuccessful, too much precipitate formed. More water was therefore added to bring the material already precipitated again into solution. Addition of alcohol then gave a precipitate 2R21 (2·02 g.). The mother liquors yielded with excess alcohol fraction 2R22 (0·98 g.). The less soluble of these two fractions, 2R21, was dissolved in 50 ml. of water and fractionally precipitated with alcohol, yielding a less soluble fraction 12R21 (0·7 g.) and a more soluble one 22R21 (1·26 g.). The subsequent fractionation of 12R21 need not be described in detail. It will suffice to say that it ultimately yielded two fractions with tyrosine contents of 1·73 and 1·37 % respectively for the less and more soluble ones. Fractions 22R21 and 2R21 were united and termed R3. Fractionation of this in the usual manner gave R31 (1·25 g.), tyrosine content 1·08 %, and R32 (0·92 g.), tyrosine content 0·38 %. R31 then yielded 1R31 (0·32 g.) and 2R31 (0·68 g.). The two more soluble fractions R32 and 2R31 were, apparently unfortunately, united and termed R4 (1·6 g.). Fractionation of this gave R41 (0·67 g.) and R42 (0·81 g.) with a tyrosine content of 0·39 %. The more soluble fraction obtained by refractionation of R41 had a tyrosine content of 1·1 %. Refractionation of R42 gave, finally, 1R42 (0·22 g.), tyrosine content 0·55 %, and 2R42 (0·52 g.), tyrosine content 0·31 %. The latter fraction was probably not homogeneous, but further fractionation by the above methods seemed impracticable. In view of the very low tyrosine content of 2R42 it is not excluded that this amino-acid was due to the presence of an impurity, possibly the main histone, and that the protein of which 2R42 is mainly composed is free from tyrosine. In any case, 2R42 consists essentially of a protein quite different in its composition from the main histone, as the following analysis shows: N content, 14·35, 14·46 %; amide-N, 1·99 % of total N; arginine-N, 8·05 % of total N. Despite its low arginine content, we nevertheless class this protein as a histone because it is a basic protein which originates from the cell nucleus. That it possesses basic properties is shown both by the method used for its extraction from the nucleus and by the presence of sulphate ions in the hydrolysate used for the arginine estimation. As will be shown below, its basic properties are largely due to a high content of lysine.

THE AMINO-ACID COMPOSITION OF HISTONES AND PROTAMINS

The amino-acids of which the various histones examined are composed have been determined as far as possible by paper chromatography, using a procedure almost identical with that originally described by Consden, Gordon & Martin (1944). When sufficient of the hydrolysate prepared for the arginine determination was available, this was used for the chromatographic analysis. Alternatively, 10 mg. of the histone sulphate were hydrolysed under conditions similar to those employed for the larger quantities. One ml. of the larger, or the whole of the smaller, hydrolysate was evaporated *in vacuo* on a water-bath almost to dryness, the residue twice redissolved in water and again evaporated, and the final residue taken up in a small volume of water and 'desalted' electrolytically (Consden *et al.* 1947) to remove the last traces of hydrochloric acid. The residue from the evaporation of the solution of amino-acids so obtained was then dissolved in 0·4 ml. of 70 % aqueous alcohol and 0·01 or 0·015 ml. of this used for each chromatogram. Two-dimensional chromatograms were finally adopted using Whatman's no. 4 paper and selecting phenol and collidine as the most useful solvents. In some of the early experiments, phenol removed a considerable amount of brown impurity from the paper, which caused a haphazard movement of the fast-running amino-acids. Spraying the entire breadth of the paper with the phenol solvent at a level immediately below the point of application of the amino-acid solution, and for a depth of about 4 in., immediately before the development of the chromatogram with this solvent diminished, but did not entirely abolish, this difficulty when the two solvents were used in the order collidine-phenol. By reversing this order, however, spraying became entirely effective. The chromatogram was run first in phenol for about 20 hr. in a cabinet containing, in addition to the normal solvents (phenol and water containing sodium cyanide), a few drops of 0·88 ammonia in the tray beneath the paper. During this time, much of the brown impurity had accumulated in the vicinity of the advancing front and had reached the bottom of the paper. After drying the paper, development was carried out with collidine, with a few drops of diethylamine in the tray, for nearly 8 days. The slow movement of the amino-acids, which rendered necessary this long period of development, proved to be an advantage, for the impurities which the solvent dissolved out of the paper were carried far in advance of the amino-acids and, together with the accumulated brown material from the phenol run, were removed entirely from the paper in the drops of solvent which fell into the tray after the advancing front had reached the end of the paper

The chromatograms obtained from the hydrolysates of the main histones from calf thymus gland, ox spleen and liver, salmon liver, cod sperm and a human tumour were indistinguishable from one another Figure 3, plate 20, which reproduces the chromatogram obtained from the main histone from cod sperm, thus serves to illustrate this group Those from the main histones of fowls' erythrocytes, thymocytes and lymphocytes were essentially similar except for the absence of phenylalanine The subsidiary histone with a high arginine content obtained from the nuclei of fowls' erythrocytes was indistinguishable qualitatively from the main histones of this species On the other hand, the subsidiary histone with a low arginine content obtained from calves' thymocytes gave a chromatogram, reproduced in figure 4, plate 20, which not only differs qualitatively from that of the main histone by lacking phenylalanine, tyrosine and histidine and containing methionine, but also indicates a marked quantitative difference in amino-acid composition As is evident from figure 4, the low arginine content of this histone is compensated for by a high lysine content, to which its basic properties must be largely due It also differs from the main histone in containing, relatively to the other amino-acids, high amounts of alanine and proline

From the above results it is evident that the main histones from cod sperm, salmon liver, calves' thymus glands, ox spleen, ox liver and a human tumour resemble one another in containing the amino-acids aspartic and glutamic acids, glycine, serine, alanine, threonine, proline, valine, the leucines, tyrosine, phenylalanine, arginine, histidine and lysine in much the same relative proportions, while the histones, including the subsidiary histone with a high arginine content, from fowls' erythrocytes, thymus glands and spleens are distinguished from these by the absence, at any rate from the chromatogram, of phenylalanine Of the amino-acids which cannot be detected readily in the chromatograms of acid hydrolysates, tryptophan has been shown by separate tests (Stedman & Stedman 1947*b*) to be completely absent from all the histones, main or subsidiary, examined in this investigation The question of the sulphur containing amino-acids has not yet been fully resolved Felix & Rauch (1931) found the high content of 1 87 % of sulphur in the histone chloride which they isolated from the whole thymus gland of the calf They also stated that the unpurified material, which they regarded as the native protein, gave a nitroprusside reaction for sulphydryl groups, but that this disappeared when it was purified through the picrate. We have examined the main histones prepared in this investigation for the presence of free sulphydryl groups by dissolving 20 mg of the histone sulphate in 1 ml of water and treating the solution with three drops of freshly prepared 5 % sodium nitroprusside and three drops of 10 % sodium cyanide An immediate magenta colour was given by every main histone with the possible exception of that from wheat germ, which gave a faint pink colour It thus seems certain that cysteine is present in the main histones. So far, however, we have obtained no evidence of the presence of methionine. Its presence in the subsidiary histone from calves' thymocytes is evident from the chromatogram; no corresponding spot has, however, been observed in the chromatograms of the main histones. It is just possible that it has been masked by the adjacent spot of the leucines which are present in high amount, although this seems doubtful According to Allgén (1950) however, it is present in thymus histone prepared from the whole gland of the calf This may be due to a contaminant from the cytoplasm or to the presence of a subsidiary histone In a communication which followed the publication (Stedman & Stedman 1950*a*) of a summary of a few of the results now described, Hamer (1951) has recorded a complete amino-acid analysis of thymus histone from the calf and stated that no cysteine or cystine could be detected in it No mention is made of methionine

The chromatograms of clupeine and salmine are of special interest, for these two protamins have, in the past, formed the subject of numerous investigations This has doubtless been due to their low molecular weights, which cause them to differ from other proteins in forming true solutions in water They were at first thought to be identical, but a definite difference between them was apparently detected when Kossel and Dakin (see Kossel 1928) found that alanine was present in clupeine but absent from salmine According to this older work, clupeine was composed of arginine, alanine, serine, valine and proline, while the amino-acids present in salmine were arginine, serine, valine and proline The subsequent work on clupeine has been marred either by the use of impure material or by the partial decomposition of the base by fractionating it in hot solution (see p 587), while work on salmine has usually been made on commercial preparations, the history and method of preparation of which cannot be known Using such material, Block & Bolling (1945*b*), in their amino-acid analyses, accounted for 100 % of the nitrogen of salmine In this work they detected the presence for the first time of alanine and small amounts of isoleucine, results which were later confirmed by Tristam (1947) who also detected, again for the first time, the presence of glycine Tristam's analyses accounted for 99 3 % of the total nitrogen The discovery of the presence of alanine in salmine removes the principal proof which has hitherto existed of the non-identity of salmine and clupeine While the arginine contents of the two proteins are, as shown in table 5, different, they are nevertheless so close to one another as to fall almost within the limits of experimental error In order to confirm the difference between them we have submitted the preparations III X1 of salmine and II V*b*1 of clupeine to chromatographic analysis with the following results Salmine was found to contain glutamic acid, serine, glycine, alanine, arginine, proline and valine It should be noted that our results differ from Tristam's in that glutamic acid is present and isoleucine absent. The amount of glutamic acid indicated in the chromatogram is small relatively to most of the monoamino-acids, but so also is that of alanine. If, therefore, glutamic acid is to be attributed to an impurity, alanine must probably be placed in the same category There is, however, no reason to suspect the purity of the salmine The amino-acid composition of clupeine differs from that of salmine It contains: glycine, serine, alanine, threonine, arginine, proline, valine and isoleucine (or leucine) The amounts of glycine and isoleucine present were, however, small

The small fraction X2, obtained from the mother liquors from the purification of salmine, contained the amino-acids. aspartic and glutamic acids, glycine, serine, alanine, lysine, arginine, proline, valine and isoleucine (or leucine) This was almost certainly contaminated with a small quantity of salmine, but the presence of lysine and other amino-acids which are not present in salmine suggests that it may contain a protein of the nature of a subsidiary histone. The presence of this protein might well account for the isoleucine found in Block & Bolling's and Tristam's preparations of salmine

DISCUSSION

There remains for discussion the question of the significance of the cell specificity, demonstrated in the course of this investigation, of the basic proteins present in cell nuclei Before considering this problem, however, it should be pointed out that these basic proteins constitute quantitatively major components of cell nuclei, for they represent from 20 to 30 % of the dry weight of the various nuclei examined As such they must in part be responsible for the formation of one or other of the chief structures of the nucleus It has been shown elsewhere (Stedman & Stedman 1947*a*, *b*) that, in combination with nucleic acid, they do, in fact, form the nuclear sap in the resting and prophase, and the spindle in the metaphase, nucleus For the exercise of such structural functions, which cannot of course be wholly divorced from physiological ones, cell specificity would presumably be inessential In order to gain some insight into the meaning of the specificity it is therefore necessary to attempt to visualize the more purely physiological functions of the basic proteins Unfortunately, the mechanism by which the nucleus itself exerts its functions, whatever these may be, is little understood Nevertheless, it is a principle of cytogenetics that each nucleus of an organism contains at least one set of the chromosomes, and hence all of the genes, of that organism It is, therefore, presumably through the activity of these hypothetical units that the function of the nucleus must be exercised There is, however, one difficulty inherent in this view If all the genes are active in every nucleus of an organism, any one nucleus would be physiologically identical with another The action of individual genes would not then be limited, as the evidence indicates that they are, to certain types of cells but would extend to every cell in the organism Moreover, it would be impossible on the chromosome theory of heredity to account for cell differentiation, for this process implies that different groups of genes are active in different types of cells The unequivocal demonstration in this work of the cell specificity of histones and protamins in at least some cells shows that although, as would be expected from cytological theory, cell nuclei do resemble one another closely in general chemical composition, there are nevertheless differences in the composition of the basic proteins in the nuclei of cells of different types This must be associated with differences in the physiological properties of these nuclei and, if it is correct that the functions of a nucleus are due to the genes which it contains, it follows that the action of the basic proteins in modifying the properties of the nucleus must be exercised through an action on the genes. We therefore advance the hypothesis that the basic proteins of cell nuclei are gene inhibitors, each histone or protamin being capable of suppressing the activities of specific groups of genes Such an hypothesis will, we believe, not only serve to explain the different properties of cell nuclei, but will also give some indication of the mechanism by which the nucleus effectively participates in the process of cell differentiation

We have to acknowledge with thanks Grants from the Royal Society and the Medical Research Council which have, in different ways, assisted this investigation. We should also like to thank Dr Helen Russell of the Christie Hospital and Holt Radium Institute for providing us with the human tissue used, Dr A. W Greenwood and Miss J. Peace of the Poultry Research Centre for the supply of chickens, and Mr G J Dutton of this Department for procuring the salmon livers.

Description of Plate 20

Figure 1 Wet smear of finished preparation of salmon sperm heads Stained methylene blue. (Magn. × *ca* 200)

Figure 2 Salmon sperm heads after treatment with 70% alcohol Stained methylene blue (Magn × *ca.* 700)

Figure 3 Paper chromatogram of amino-acids from the histone isolated from the sperm heads of the cod (1) aspartic acid, (2) glutamic acid, (3) glycine, (4) serine, (5) alanine, (6) threonine, (7) lysine, (8) arginine, (9) histidine, (10) proline, (11) valine, (12) the leucines with, possibly, methionine, (13) phenylalanine, (14) tyrosine

Figure 4 Paper chromatogram of amino-acids from the subsidiary histone isolated from nuclei from the thymus gland of the calf (1) aspartic acid, (2) glutamic acid, (3) glycine, (4) serine, (5) alanine, (6) threonine, (7) lysine, (8) arginine, (10) proline, (11) valine, (12) leucine or isoleucine, (15) methionine

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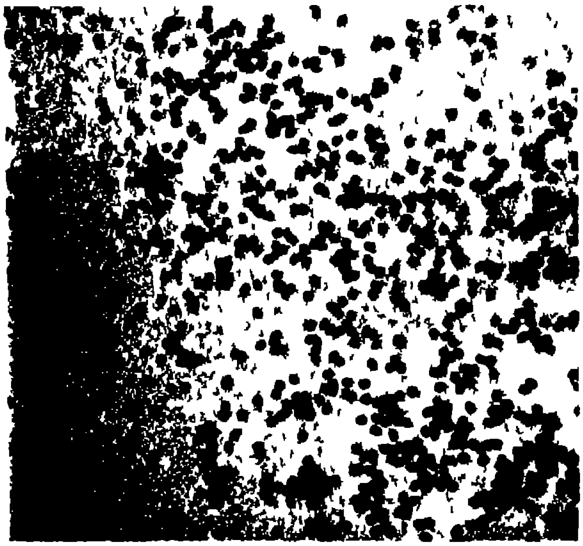

FIGURE 1

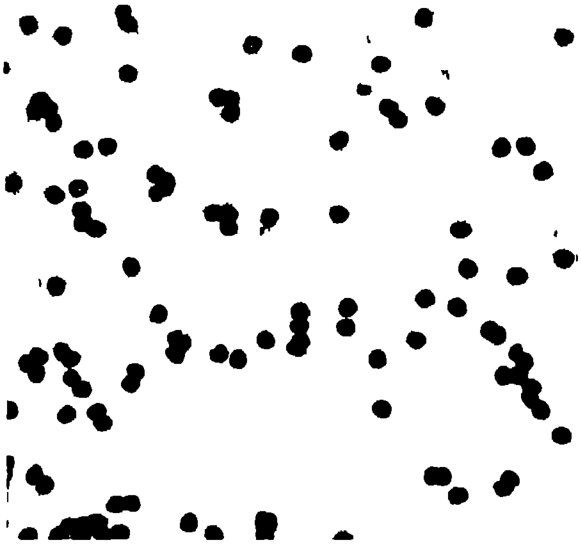

FIGURE 2

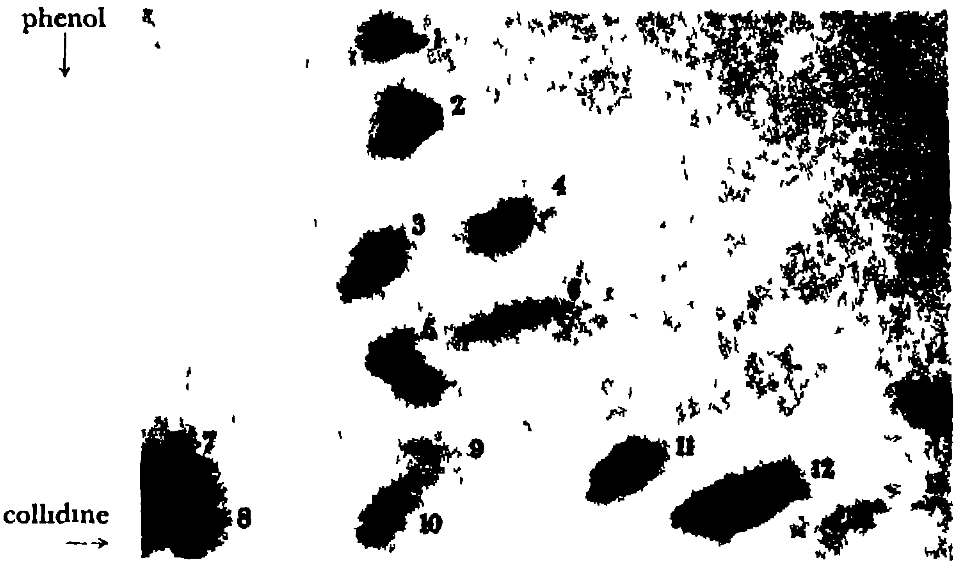

FIGURE 3

FIGURE 4

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